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Thesis of
KATELYN KLUG

Submitted in Partial Fulfillment of the Requirements for the Degree of

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Halmos College of Natural Sciences and Oceanography

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

CROSS-SHELF AND LATITUDINAL BENTHIC COMMUNITY INVESTIGATION IN THE NEARSHORE HABITATS OF THE NORTHERN FLORIDA REEF TRACT

By

Katelyn Klug

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

Marine Biology &
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ABSTRACT

The Florida Reef Tract (FRT) extends from the tropical Caribbean northward along the Florida coast into a warm temperate environment where tropical reef communities diminish with increasing latitude. This study was designed to map the nearshore benthic habitats including coral reefs and evaluate how the benthic communities differ between habitats and along the coast.

Benthic communities across the northern FRT from Key Biscayne to Hillsboro Inlet (25.5°-26.3° N) were digitized from aerial photography taken in 2013 at a 1:1,000 scale. Three main hard-bottom habitat types were identified that ran parallel to shore and consecutively further away from shore: Colonized Pavement, Ridge, and Inner Reef. Five 1-km wide cross-shelf corridors (numbered 1-5, south to north) were designated and spaced as evenly as possible throughout the region. Five sites per habitat per corridor (70 total) were randomly selected and quantitative data collected within 4,200 m^2.

Significant differences in percent benthic cover among habitats were found in all corridors and within habitat types between corridors, indicating cross-shelf and latitudinal variation. Mean stony coral density increased with depth, with the Inner Reef habitat being significantly higher than both the Colonized Pavement and Ridge. Mean stony coral species richness also increased with depth, with all habitats significantly different from one another. A total of 22 stony coral species were identified within the mapped region, the three most abundant being *Porites astreoides, Siderastrea siderea,* and *Acropora cervicornis*.

Results from this study support the ecosystem regions denoted in the Walker (2012) study. Corridor 1, located in the Biscayne Region, was the only corridor to contain any seagrass. In addition, Corridor 1 Inner Reef had significantly higher values for mean stony coral density, mean stony coral species richness, mean gorgonian density of the plume morphotype, and mean density of stony corals infected with *Cliona* spp. Corridors 2-4, located in the Broward-Miami Region, had some variability associated with them, but were generally similar in benthic composition. Corridor 5, likewise located in the Broward-Miami Region but in close proximity to the Deerfield Region, also had differences associated with it. Both the Colonized Pavement and Ridge habitats in Corridor 5 had the lowest mean coral species richness, as well as total absence of both sponge species noted in this study. Corridor 5 Inner Reef also had significantly lower mean stony coral densities compared to Corridors 1, 2, and 4. As such, these results support the idea of different biogeographic regions occurring off the southeastern Florida coast.

This study produced two key findings. It discovered over 110 large (>2 m) resilient coral colonies, of which 50 were alive in various conditions. This study also found 38 acres of dense *Acropora cervicornis* patches, tripling the previously known area within the study region. These are the largest dense patches in the continental United States.

Keywords: Northern Florida Reef Tract – Latitudinal – Benthic communities – Biogeographic regions – Nearshore habitats

1. INTRODUCTION

1.1 Status of Coral Environments around the World

Around the world, coral reefs are faced with natural and anthropogenic impacts that are becoming increasingly more severe (Birkeland 1997; Connell *et al.* 1997; Bryant *et al.* 1998; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Wilkinson 2004; Hoegh-Guldberg *et al.* 2007; Carpenter *et al.* 2008). These ecosystems contain the highest biodiversity of any in the marine environment, and provide essential habitat for a plethora of sessile and mobile organisms. Economically they are valuable, as they provide coastal communities with extensive tourism, seafood resources, and shoreline protection from tropical storms.

Coral reefs are currently threatened by rising sea temperatures. Since the start of the 20th century, global average temperature has risen 0.9°C (IPCC 2014). In the past 25 years, sea surface temperatures have exceeded normal summer maxima by 1 or 2° C for at least 4 weeks in various locations throughout the Caribbean (Wilkinson and Souter 2008). Shallow-water corals and numerous other benthic invertebrates maintain a symbiotic relationship with algae known as zooxanthellae (Brant 1881). Zooxanthellae photosynthesize inside their hosts and provide energy and nutrients by translocating up to 95% of their photosynthetic production to their symbiotic partner (Muscatine 1990). When temperatures exceed normal tolerance ranges for an extended period of time, the zooxanthellae produce an excessive amount of toxic compounds that are transferred to the coral host (Douglas 2003). Corals react by expelling their symbiotic algae, a process known as bleaching, leaving the coral white and particularly susceptible to death from starvation or disease (Brown 1997, Douglas 2003). These algae provide much of the energy required for coral reef growth. If temperatures continue to rise, episodes of coral bleaching and disease will continue to increase in frequency and magnitude (Kleypas *et al.* 1999, Hoegh-Guldberg 1999, Knowlton, N. 2001; Harvell *et al.* 2002). If conditions improve, it is possible for corals to recover; however, they will often experience reduced growth and may skip reproduction efforts during the following season (Wilkinson and Souter 2008).

Ocean acidification is another climate-related factor that may threaten corals. Increased concentrations of dissolved CO_2 increase seawater acidity by reducing the pH level. Increased dissolved CO_2 also reduces the level of saturation of the carbonate mineral aragonite (Orr *et al.* 2005) that reef corals depend on for producing their skeletons (Kleypas *et al.* 1991). As the oceans absorb more CO_2, impacts on marine calcifiers could be considerable (Wilkinson and Souter 2008). Laboratory studies using pH levels expected by the end of this century show a significant reduction in the ability of reef-building corals to deposit their carbonate skeletons, slowing their growth and increasing their vulnerability to erosion. This weakening of coral skeletons and reduced accretion of reefs is predicted to be greater at higher latitudes (Kleypas *et al.* 1999). Though long-term consequences of ocean acidification on corals are not known, it does not appear that corals will easily adapt to such rapid changes (Wilkinson and Souter 2008).

Within the past three decades, scleractinian coral cover in Caribbean reefs has declined by an estimated 80% (Gardner *et al.* 2003; Wilkinson 2004; Wilkinson 2008). This decrease is a result of warming sea temperatures and other factors including increased coastal development, sewage discharges, sedimentation, and nutrient enrichment resulting from poor land-use and watershed management (Banks *et al.* 2008). The addition of nutrients can lead to shifts in algal community structure, which results in coral communities being overgrown by fleshy turf species (Szmant 2002). Quantitative, small-scale studies have described changes such as reduced coral cover, reduced physical and biological diversity, and increases in the spatial and temporal extent of macroalgae throughout the Caribbean (Ginsburg 1993; Hughes 1994). Given increasing human populations near coral reefs, the growing threat of climate change to coral survival and reef framework building, and the potential synergy between these threats, it is critical to conserve local areas of high coral cover, which could play an important role as a refuge and as a source of larval supply for degraded sites (Edmunds 2002).

1.2 Habitat Shifts with Climate Change

Common climate change scenarios predict that a doubling of CO_2 from pre-industrial levels will result in an increase in temperature of 2 - 4°C at the equator and 6 - 9° C at higher latitudes (50-70°N) (Manabe *et al.* 1991; Viner *et al.* 1995). These atmospheric temperature changes will influence latitudinal and vertical shifts in oceanic water temperature (Manabe *et al.* 1991). Given the influence of temperature on the survival, reproductive success, dispersal patterns, behavior and competitive advantage of marine species, a 2°C rise in temperature will undoubtedly lead to considerable changes in marine communities (Southward *et al.* 1995). If global warming results in a shift of tropical water masses and their resident biota toward the poles, species ranges will be limited by their ability to survive changing temperatures (Engle and Summers 1999). Reactions by marine organisms to temperature change will vary among species, and not all will shift their distributions in response (Fields *et al.* 1993). Different species tolerate different temperature ranges. As examples, stenothermal taxa have narrow ranges; the Antarctic bivalve mollusc *Laternula elliptica* can only survive between 5 and 12°C above the minimum sea temperature of -2°C (Peck *et al.* 2004). By contrast, eurythermal taxa may have quite broad ranges; the ctenophore *Mnemiopsis leidyi*, tolerates temperatures ranging from 4.0 to 31.0 °C (Shiganova 1998). Species that can survive changing conditions either adapt genetically or live under suboptimal conditions (Fields *et al.* 1993). Distributional shifts may also include vertical displacements to deeper, cooler waters in response to anthropogenic warming (Hubbs 1948). Thus, the ability of each species to survive in the face of environmental temperature change is strongly dependent on that species' mobility and past thermal adaptations (Fry 1971).

The idea of redistribution as a result of thermal change may not be possible for all marine communities. Geographical barriers may restrict some species from migrating (Fields *et al.* 1993). Even in the absence of geographical barriers, some species may be prevented due to a lack of necessary physical resources such as appropriate substrate, nutrient levels or nursery grounds for settling larvae (Fields *et al.* 1993). Tropical corals will be particularly affected by increased sea surface temperatures, as so many species currently exist close to their upper thermal tolerances (Glynn 1991).

1.3 Southeastern Florida reefs

The Florida Reef Tract (FRT) runs along the shelf margin of the continental southeastern United States from the Dry Tortugas to the St. Lucie River Inlet (27.25°N), and includes the Florida Keys and Biscayne National Park. It is the third largest reef system in the world and the largest in the continental United States.

The FRT has been subject to losses in stony coral cover and species abundance (Porter and Meier 1992; Wheaton *et al.* 2001; Porter *et al.* 2002). Porter and Meier (1992) surveyed six coral reef locations between Key West and Miami, FL and found that all six areas exhibited declines in coral species diversity during the time the areas were surveyed with losses constituting between 13% and 29% of species richness, along with sustaining significant losses in coral cover. Areas of live *Acropora palmata* and *Acropora cervicornis* at Looe Key declined by 93% and 98%, respectively, between 1983 and 2000 (Miller *et al.* 2002). The Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP), which provides annual assessments of the southeastern Florida reef system, found that mean stony coral cover was below 5% within 10 region-wide sites since 2008 (Gilliam *et al.* 2013).

This project focuses on the northern Florida Reef Tract (nFRT), which spans approximately 170 km of southeastern Florida coastline from Miami (25.5°) to St. Lucie Inlet (27.2°) and supports a diverse coral reef community (Walker and Gilliam 2013). However, the arrangement of seafloor habitats varies significantly within this region (Walker 2012). Like the Florida Keys, the nFRT formed as a result of Holocene sea-level rise. During the Holocene, an extensive *Acropora palmata* barrier reef flourished off southeastern Florida (Lighty *et al.* 1978). From Miami to Broward County, a series of three shore-parallel, progressively deeper, reef-like ridges or terraces exist but exhibit little to no active accretion due to exceedingly low reef building coral cover (Moyer *et al.* 2003). All of these reefs were progressively drowned as sea level rose (Lighty 1977), and they are now capped by a veneer of living coral and other reef organisms where most of the vertical relief structure is relict (Marszalek *et al.* 1977). Regional terminology and previous literature have referred to these Miami-Broward linear ridge habitats as "reefs" (Light *et al.* 1978; Moyer *et al.* 2003; Banks *et al.* 2007; Gilliam *et al.* 2007; Sathe *et al.* 2008; Walker *et al.* 2008). Lighty (1977) and Walker *et al.* (2008) referred to the Inner, Middle, and Outer reefs together as the 'Reef Complex.' This linear reef system is relatively continuous, runs parallel to shore, and consists of a rich coral reef community, which crests at approximately 8 m depth.

The Inner Reef begins in northern Broward County and ends in North Miami-Dade County. Shoreward of the Inner Reef lies the Nearshore Ridge Complex (Lighty 1977; Moyer *et al.* 2003; Walker 2012), a combination of colonized pavement and ridges found shallower than 10 m depth. The colonized pavement habitat extends from Hillsboro Inlet in Broward County (N 26°15') south to Miami-Dade County (N 25°51'). The colonized pavement habitat is mainly a contiguous area of solid carbonate rock that supports assemblages of macroalgae, scleractinians, gorgonians, and other sessile invertebrates. This habitat also includes areas of rubble and is subject to variable sand cover, which shifts in response to weather-generated wave energy. Thus, areas of the colonized pavement will occasionally be covered by shifting sand and the colonization density of benthos will vary accordingly. The ridges, which are linear and parallel, low-relief features that extend from Hillsboro Inlet (N 26°15') through Broward County but taper off north of Government Cut (N 25°45') are believed to be submerged cemented ancient shoreline deposits (Banks *et al.* 2007). This intricate limestone system has visible karst features supporting a biological assemblage similar to that of colonized pavement: macroalgae, scleractinians, gorgonians and other sessile invertebrates dense enough to obscure the underlying carbonate rock. It is important to note that the ridge habitat has a relatively high mean percent coral cover (approximately 12%) with uniquely large colonies of a few dominant species, including *Montastrea cavernosa, Orbicella* spp., and *Siderastrea siderea* (Gilliam *et al.* 2005).

The nFRT contains approximately 85 km² of significant, economically and ecologically valuable coral reef communities existing in 2 - 5 m water depths between Hillsboro Inlet and Key Biscayne (Walker 2012). The habitats within the nFRT are dominated by a combination of algae, scleractinians, octocorals, *Palythoa* spp., and sponges, which therefore include some of the most valuable submerged resources in Florida (Goldberg 1973, Moyer *et al.* 2003, Gilliam *et al.* 2013). Coral communities in southeastern Florida consist of typical Caribbean fauna, although community structure does not conform to existing reef classification schemes (Goreau 1959). Though species richness mirrors that of the rest of the Caribbean, density and distribution do not (Moyer *et al.* 2003). The biological communities of these reefs are also highly variable, which may be due to their high-latitude location, freshwater runoff, groundwater seepage, sewage effluent and tidal inlet discharge (Goldberg 1973), and high variability of substratum composition and complexity (Moyer *et al.* 2003). Frequent hurricanes and tropical storms may also contribute to this variability (Muller and Stone 2001). These reefs also have a different community structure than those further south along the Florida Reef Tract and in other areas in the Caribbean, including the Bahamas, Jamaica and Puerto Rico (Moyer *et al.* 2003). Average coral size is small (typically <50 cm in diameter) and relative percent cover by scleractinians is low (< 6%) with the exception of several shallow nearshore limestone ridges having relatively high cover (roughly 12%) (Moyer *et al.* 2003) and a few with coral coverage >40% in some parts (Gilliam *et al.* 2013). Though variable, the nFRT has significant features including over 50 recently discovered live coral colonies greater than 2 m diameter (some up to 4 m and over 300 years old) (Walker, unpublished). In addition, Walker and Klug (2014) recorded 35 extensive monospecific aggregations of the threatened scleractinian *Acropora cervicornis*.

The nFRT exists within 3 km of the coast and is located off a highly urbanized area influenced by numerous impacts including commercial and recreational fishing and diving, shipping ports, sewer outfalls, canal discharges, ship grounds, and marine construction activities (Banks *et al.* 2008). This region has undergone some of the most rapid human population growth of any area of the United States (Culliton *et al.* 1990). Concomitant with human population growth has been the development of major ports and inlets, and the hardening of most of the estuaries for flood control. Shoreline modifications, including channelization, levee building, shoreline armoring, and wetland removal, may have serious consequences that limit riparian zone interactions, change flow patterns, alter invertebrate communities, and decrease heterogeneity on many scales (Johnson *et al.* 1995). The development of major ports in the 1920's and shipping activity since has impacted coral reefs and hardbottom habitats substantially (Walker *et al.* 2012). Port development, along with increased vessel activity, can have destructive effects on benthic communities, particularly coral reefs, as they rely on hard framework that may take thousands of years to form (Walker *et al.* 2012). Due to the high economic and recreational value of beaches (Johns *et al.* 2004), substantial marine dredging and fill projects frequently widen local beaches that are subject to erosion (ACOE 1996). This erosion is one result of inlet development, which alters the effects of ocean waves, currents and movement of sand southward along the coast (Reeve *et al.* 2004). As a result, nearshore hardbottom habitats, which represent a large portion of local natural reef structures, are often buried or indirectly affected (Lindeman 1999). Since the nearshore hardbottom features lie within 200 m of the shore between estuarine habitats and linear reefs, they serve as settlement grounds for immigrating larvae or nursery habitats for juveniles emigrating out of inlets (Vare 1991; Lindeman 1999). In addition, these habitats house many significant coral reef resources, including octocorals, sponges, and threatened and endangered scleractinian coral species (Walker and Klug 2014). When these habitats are negatively affected by anthropogenic factors, many organisms, particularly corals, suffer, as they require specific environmental conditions for growth and survival (Osinga *et al.* 2011). The nFRT tract nearshore benthic habitats' high ecological and economic value and proximity to threats require characterization of the component benthic communities.

A current snapshot of shallow-water coral communities is essential to determining impacts from both permitted (e.g., coastal construction) and accidental (e.g., groundings, oil spills) impacts. Benthic community data have been identified as a need by multiple managers in southeastern Florida and will be used to directly reduce impacts to coral reef and hardbottom resources from local coastal construction projects (e.g., beach nourishment) through the design and review of permit applications. These data can also be used to reduce un-permitted impacts by informing marine zoning efforts and supporting creation of new no-anchor zones.

1.4 Northern Florida Reef Tract Latitudinal Gradient

The nFRT is unique in that it straddles different climate regimes (Walker 2012). The reef system transitions from a tropical to temperate Holdridge Life Zone (Lugo *et al.* 1999), where several estuarine biogeographic zones have been defined (Engle and Summers 1999). Recent analyses have identified several biogeographic spatial barriers where the number of benthic habitats attenuated northward along the coast and various habitat metrics differed significantly between six sub-regions (Walker and Gilliam 2013; Walker 2012). From south to north, the environment, associated habitats and organisms gradually shift from tropical to a warm temperate. This phenomenon is pervasive throughout the literature of global patterns of organism distributions. Such latitudinal gradients have long been used as general biogeographic indicators of the distribution, community composition, and diversity of marine organisms (Briggs 1974; Hayden and Dolan 1976; Stevens 1989; Calder 1992; Rapoport 1994; Engle and Summers 1999). In the marine environment, latitude is a surrogate for numerous environmental gradients, such as temperature, seasonality (Willig 2003), and pH (Steinacher *et al.* 2009). The tendency for species richness to increase with decreasing latitude has been reported in many studies (Wallace 1878; Dobzhansky 1950; Fischer 1960; Pianka 1966). One popular explanation for this trend is the “species richness-energy hypothesis,” which indicates that the number of species that can coexist in a zone is limited by energy supply (Macpherson 2002). The energy availability depends on the mean temperature or factors that are strongly linked to it (Roy *et al.* 1998). Marine organisms tend to have larger ranges and exhibit distinct latitudinal zonation more frequently in comparison to terrestrial fauna (Engle and Summers 1999). This is especially true in near-shore environments where physical barriers prevent the migration of littoral species (Pielou 1979; Rapoport 1994). Chemical, spatial, and biological barriers can also be present (Hayden and Dolan 1976), along with numerous oceanic factors such as local upwelling intensity (Connolly and Roughgarden 1998; Walker and Gilliam 2013).

Engle and Summer (1999) recognize two primary views of the driving forces for latitudinal gradients in the distribution of species. One is that temperature or climate is the primary force and that marine communities tend to coincide with oceanic provinces, which are distinguished by prevailing currents and temperature (Hutchins 1947; Hall 1964; Cerame-Vivas and Gray 1966). The second is that geographical or physical barriers coincidentally associated with climatic factors provide major breakpoints in the latitudinal distribution of species (Hayden and Dolan 1976; Golikov *et al.* 1990; Vermeij 1991).

Reef-building coral distributions are limited by their requirements for warm temperatures and high light availability (Muir *et al.* 2015). Photosynthesis, heterotrophic feeding, and calcification also influence coral growth and success (Osinga *et al.* 2011). Johannes (1983) also suggested that latitudinal limits of coral growth are generally determined by competition from macroalgae. Higher latitudes favor many species of benthic algae due to associated high nutrient concentrations, moderate water temperatures, and, possibly, reduced grazing pressure, while lower temperatures reduce coral growth (Johannes 1983). Shallow-water coral communities generally extend from 30° N to 30° S of the equator. Latitudinal variation in biological communities is expected within the nFRT due to its location—25°-27° N—near the northern distributional limit of most tropical corals.

Walker (2012) showed that a latitudinal benthic habitat zonation exists along the northern Florida Reef Tract (FRT) between St. Lucie Inlet and Key Biscayne: the size and number of distinct benthic habitats decreased northward with increasing latitude. Walker (2012) defined several distinct areas, sometimes defined by recognizable coastal features that function as boundaries. The Biscayne region is the northernmost area that supports large *Thalassia* and *Syringodium* seagrass meadows. The Bahamas Fault Zone, between the South Palm Beach and North Palm Beach regions, is the northern limit of historic reef growth (Walker 2012). Here, the shelf widens northward, and the warm Florida Current moves offshore (Walker and Gilliam 2013), allowing colder northern water to bathe the coast (Walker and Gilliam 2013). The frequent upwelling events that occur in this area (Smith 1983; Pitts and Smith 1997) can cause temperatures to fluctuate by 10°C for days to several weeks (Smith 1983; Pitts 1993) and have been implicated as a cause for latitudinal differences in benthic communities (Walker and Gilliam 2013). Banks *et al.* (2008) analysis of the local ichthyofauna found that, of 400 species, 43 were restricted to the North Palm Beach region and 56 were exclusively found in the South Palm Beach region, providing additional support for a boundary in this area.

Previous local studies have indicated that species richness and evenness increase along a north-south gradient, which supports the latitudinal gradient concept (Dodge 1987; Moyer *et al.* 2003, Gilliam 2007; Banks *et al.* 2008; CSA International Inc. 2009). Currently, SECREMP, the most comprehensive and regional coral reef research project in southeastern Florida, showed a northward attenuation of scleractinian coral species from Miami-Dade to Martin counties (Gilliam *et al.* 2013). Latitudinal differences in scleractinian coral growth rates were also reported by Dodge (1987), who found that *Orbicella annularis* had higher growth rates at 9 m depth in south Broward than similar colonies in north Broward at higher latitudes. Changes in ichthyofaunal assemblages have also been reported due to latitudinal differences. Lindeman (1999) found that *Anisotremus surinamensis, Haemulon parra, Diplodus* spp., and *Labrisomus nuchipinnis* were in significantly higher abundances in the North Palm Region than further south in Broward. Kilfoyle *et al.* (2015) found significant differences between fish communities in Martin and North Palm Beach counties versus locations further south. These differences coincide with benthic communities distinguished by Walker and Gilliam (2013), who pointed out that benthic communities are explained by differences in temperature regimes along the southeast Florida coast. They found that cold-tolerant coral species dominated the more northern communities, with tropical species substantially fewer than in locations further south.

1.5 Current Mapping of the Northern Florida Reef Tract

Benthic habitat mapping activities in southeastern Florida have progressed substantially in the last decade (Banks *et al.*, 2007; Foster *et al.*, 2009; Riegl *et al.*, 2005; Walker, 2009; Walker, 2012; Walker and Gilliam, 2013; Walker *et al.*, 2008). These efforts combined a variety of techniques and data types, including laser bathymetry, aerial photography, acoustic ground discrimination (AGD), video groundtruthing, limited subbottom profiling, and expert knowledge as available (Walker *et al.* 2008). Nova Southeastern University's Halmos College of Natural Sciences and Oceanography and the National Coral Reef Institute (NCRI) led this effort with interagency funding from the National Oceanic and Atmospheric Administration (NOAA), Florida Department of Environmental Protection (FDEP), and Florida Fish and Wildlife Research Institute (FWRI). The maps were produced by outlining features in the high-resolution bathymetric data and aerial photography, and classifying the features based on their geomorphology and benthic fauna. *In situ* data, video camera groundtruthing, and acoustic ground discrimination were used to substantiate the classification of the habitats based on aerial photography and geomorphology. The maps showed high levels of accuracy comparable to those based on aerial photographs in clear water (Riegl, *et al.*, 2005; Walker, 2009; Walker & Gilliam, 2013; Walker, *et al.*, 2008).

The current maps provide a good and accurate understanding of where features are at a large scale, yet they do not provide quantitative *in situ* data on the benthic communities in those mapped areas. Further, many of these maps were based on bathymetric data collected in 2001 and 2002, which limited their ability to capture the most recent depictions of seafloor habitats. Since the creation of these maps, several higher-resolution datasets have been produced in Broward and Miami-Dade counties. In 2008, Broward County collected bathymetric LIDAR using the Laser And Depth Sounder (LADS) system. These data were collected at a higher resolution than the 2001 survey and used better post-processing algorithms to reduce survey artifacts. In 2009, NOAA’s Office of Coast Survey used the same system to collect higher-resolution data over a large area in Miami-Dade County around Government Cut and northern Biscayne Bay for charting purposes. When combined with new high-resolution aerial photography, these data would facilitate a more accurate, higher-resolution benthic habitat map. The images also provide a new baseline for the state of the resources.

The current project focused on the nearshore reef habitats of the nFRT, because they are the most vulnerable to coastal construction activities and other anthropogenic impacts. Detailed 1-ft (0.305-m) resolution overlapping aerial photographs were collected for the Nearshore Ridge Complex (NRC) and Inner Reef along 68.5 km of coastline from Key Biscayne to Hillsboro Inlet (Figure 1). The images documented the existing condition of resources and were used as the primary data for the detailed habitat mapping. The imagery and recent bathymetry were visually interpreted into benthic habitat maps using techniques similar to those of current regional mapping at a much finer resolution (0.1 ha versus the previous 0.4 ha). Additionally, a baseline habitat characterization was performed to obtain the current status of coral reef community composition.

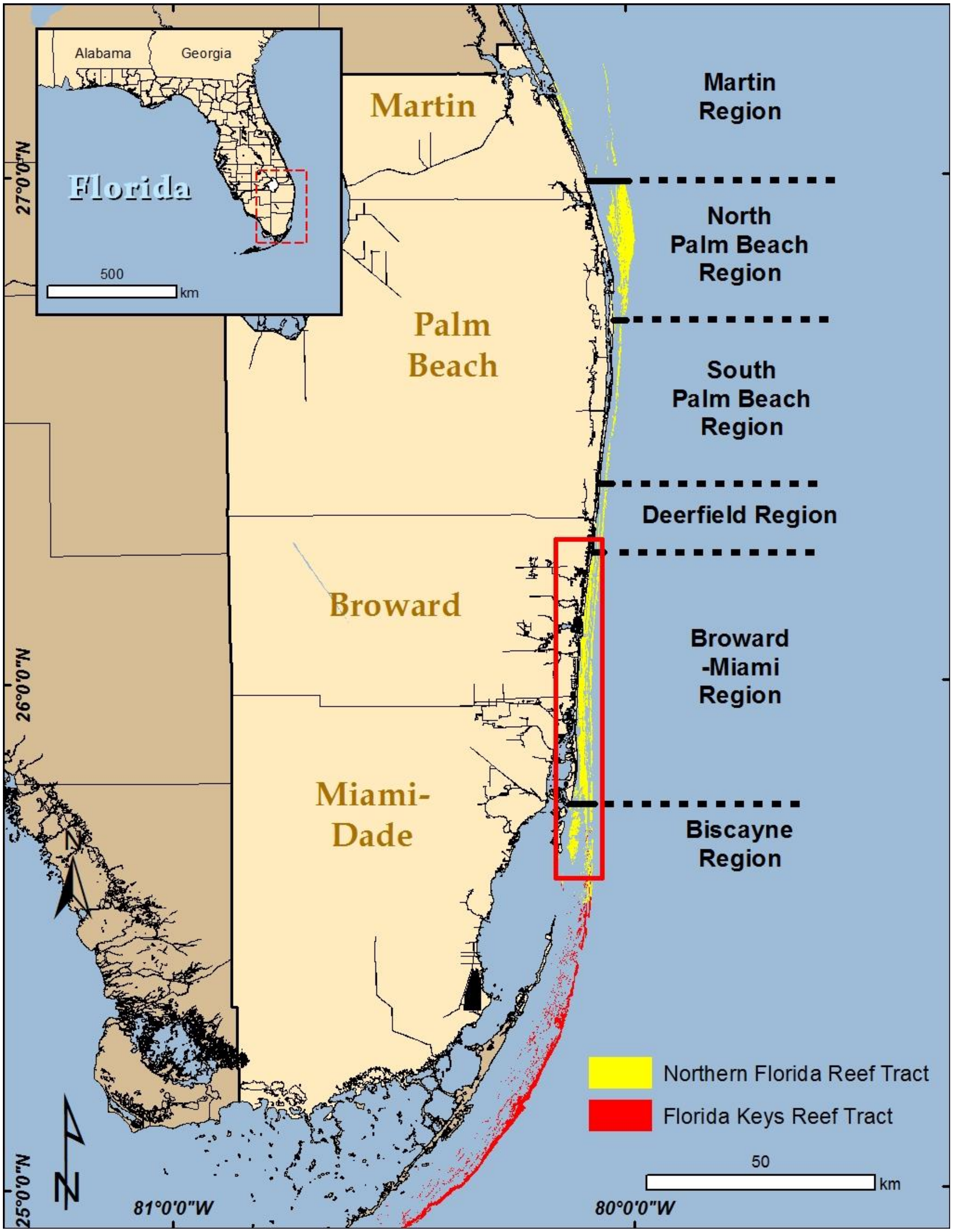


Figure 1. *Nearshore benthic habitat mapping for the current project (red box). Area includes all marine seafloor in 0 - ~10 m depth from Key Biscayne to Hillsboro Inlet.*

2. PURPOSE OF STUDY

This study created a baseline for recognizing effects of climate change as well as more local, natural and anthropogenic stressors within the region. Attention focused on such higher-latitude systems may provide evidence of range expansions and ecosystem shifts. This study provided robust data on the current extent and composition of benthic habitats on the nearshore coral reefs, facilitating detection of future responses of benthic communities to management actions and climate change. The goals of this project were to provide managers with:

1. **Increased map resolution.** Previous Broward maps were created at a 1:3000 scale and a minimum mapping unit of 0.4 ha (1 acre). This study increased the mapping resolution fourfold to 0.1ha (0.247 acre).

2. **Quantitative information on nearshore habitats.** Existing maps are based on reef morphology and inferred associated communities from previous projects, local diver knowledge, and qualitative video. The qualitative video estimations and monitoring data referenced for these maps were designed to monitor change over time, not to characterize the region. This study provides quantitative data on the major functional groups, including corals, on the nearshore habitats. A systematic regional-scale quantitative assessment of the nFRT nearshore benthic communities has never been performed. This work enables estimations of functional group cover at a level relevant to management needs (e.g., whether management decisions affected reef health).

3. **Data on the latitudinal differences in benthic communities-** Quantitative data are statistically compared between five cross-shelf corridors in two coral reef ecosystem regions to better understand how the benthic communities change with latitude along the SE Florida coast.

Addressing these goals supports the recently developed Florida’s Coral Reef Management Priorities (The State of Florida and NOAA Coral Reef Conservation

Program 2010) as follows. Goal A1 of the Priorities addresses management of the Florida Reef Tract and ecosystem using an ecosystem-based approach, including zoning/marine spatial planning and other appropriate tools. Objectives 2 and 3 of this goal are relevant to my research, as they seek to develop and implement a comprehensive zoning plan for the entire Florida Reef Tract and establish a regulatory coordination committee under the Florida Reef Tract and Ecosystem Management Council. The most recent benthic habitat map of the nearshore habitats will provide managers with the tools required to make efficient executive decisions. Goal B3 focuses on Florida Reef Tract and ecosystem climate-change-related management actions and response. Objective 3 of this goal aims to identify areas of perceived resilience (i.e., high coral cover and abundance) and areas of high vulnerability (which may or may not contain high coral cover/abundance) within the Florida Reef Tract and ecosystem and provide additional protection to those areas via appropriate marine zoning and reduction of existing stressors. Since my research examines the region from a latitudinal aspect, inferences on how the ecosystems will respond to climate change can be made. Goal C3 intends to educate the public and elected officials about the need to maintain coral reef habitats and coastal water quality. Objective 4 of this goal will establish appropriate coastal construction guidelines and educate the public and elected officials about the need to consider the impacts of coastal construction. This study will be available to both managers and the public, and illustrates the many environments that will be effected if regulations are not set in place to control coastal construction. Goal C4 intends to develop policies that will regulate coastal water quality impacts to reefs. Objective 3 of this goal seeks to build capacity and develop interagency procedures and protocols that will allow coral reef management agencies along the Florida Reef Tract and ecosystem to effectively participate in planning, review and permitting processes for development, coastal construction and water-management projects and initiatives. It is essential that these agencies be informed about what resources are present as they design protocols that regulate coastal water quality. Goal D2 is to reduce physical marine benthic impacts from recreational and commercial activities and marine debris. Objective 1 focuses on implementation of appropriate marine zoning (i.e., potential no-take zones, no-anchor zones, no-motor zones, and mooring buoy systems) and provides education and enforcement in sensitive, unique or highly productive habitat areas. Data collected during my study shows specific areas of highly productive habitat areas that will need additional conservation efforts. Goal D4 aims to reduce physical marine and benthic impacts from recreational and commercial diving and boating by implementing appropriate marine zoning for these activities. Having access to the most current nearshore benthic habitat map will provide managers with the necessary information to designate appropriate areas that avoid high areas of production.

As stated in the NOAA CRCP's National Goals and Objectives 2010-2015 report, all three (Climate Change, Fishing, and Land-Based Sources of Pollution) threat-based strategies require data to identify changes to the resource. This project will provide managers with nearshore data required to develop appropriate management strategies, track the effectiveness of these strategies, and support outreach activities, which increase stakeholder involvement. This project supports a number of Local Action Strategies in Florida's focus areas of concern (Fishing Diving and Other Uses, Land-Based Sources of Pollution, and Maritime Industry and Coastal Construction Impacts).

Thesis Objectives

- Determine if statistical differences exist among coral communities across the shelf in the nFRT nearshore benthic habitats;
- Determine if statistical differences exist in benthic cover across the shelf in the nFRT nearshore benthic habitats;
- Determine if statistical differences exist among coral communities latitudinally along nFRT nearshore benthic habitats;
- Determine if statistical differences exist in benthic cover latitudinally along nFRT nearshore benthic habitats.

3. METHODOLOGY

Benthic habitat maps of the study area were created with data assembled in ArcGIS to aid in seafloor feature identification using a combined technique approach (Walker *et al.* 2008). Many data were available; however, priority was given to the most recent datasets: 2013 aerial photography collected for this study, the 2008 Broward LADS bathymetry, and the 2009 NOAA Office of Coast Survey (OCS) bathymetry. Referencing these aerial images permitted effective delineation of edges of hard grounds, patch reefs, and seagrass beds. A high-resolution, hill-shaded, raster image of the LADS bathymetry data was used to map feature location and geomorphology of visible features. Disagreements between data types were resolved by expert-driven interpretation based on the concordance of the majority of data types, but emphasizing the most recent data.

3.1 Aerial Photography

GMR Aerial Surveys, Inc. dba Photo Science was subcontracted to collect the imagery. Images were acquired on March 8, 2013 (Figure 2). The digital orthophotography consisted of 3 bands (RGB) with a 1-ft (0.305-m) pixel spatial resolution.

3.2 LIDAR Bathymetry

Bathymetric LIDAR surveys were conducted in 2008 and 2009 using the LADS system with a sounding rate of 900Hz (3.24 million soundings h^{-1}), a position accuracy of 95% at 5-m circular error probable, a horizontal sounding density of 4 x 4 m, a swath width of 240 m, area coverage of 64 km^2 h^{-1}, and a depth range of 70 m, depending on water clarity. The 2008 survey encompassed all of Broward County and was conducted by Broward County Natural Resources Planning and Management Division (Figure 3). Full details can be found in Ramsay and Sinclair (2008). The 2009 survey was conducted by the NOAA OCS and encompassed a large area around Government Cut in Miami-Dade County (Figure 4). The processed x,y,z data were gridded by Nearest Neighbor interpolation into a digital elevation model (DEM) and masked to the data extent. The DEM was then converted to a hillshade image with the sun shaded at a 45° angle and azimuth. The DEM provided depth information, while the hillshaded image showed the three-dimensionality of the seafloor features.

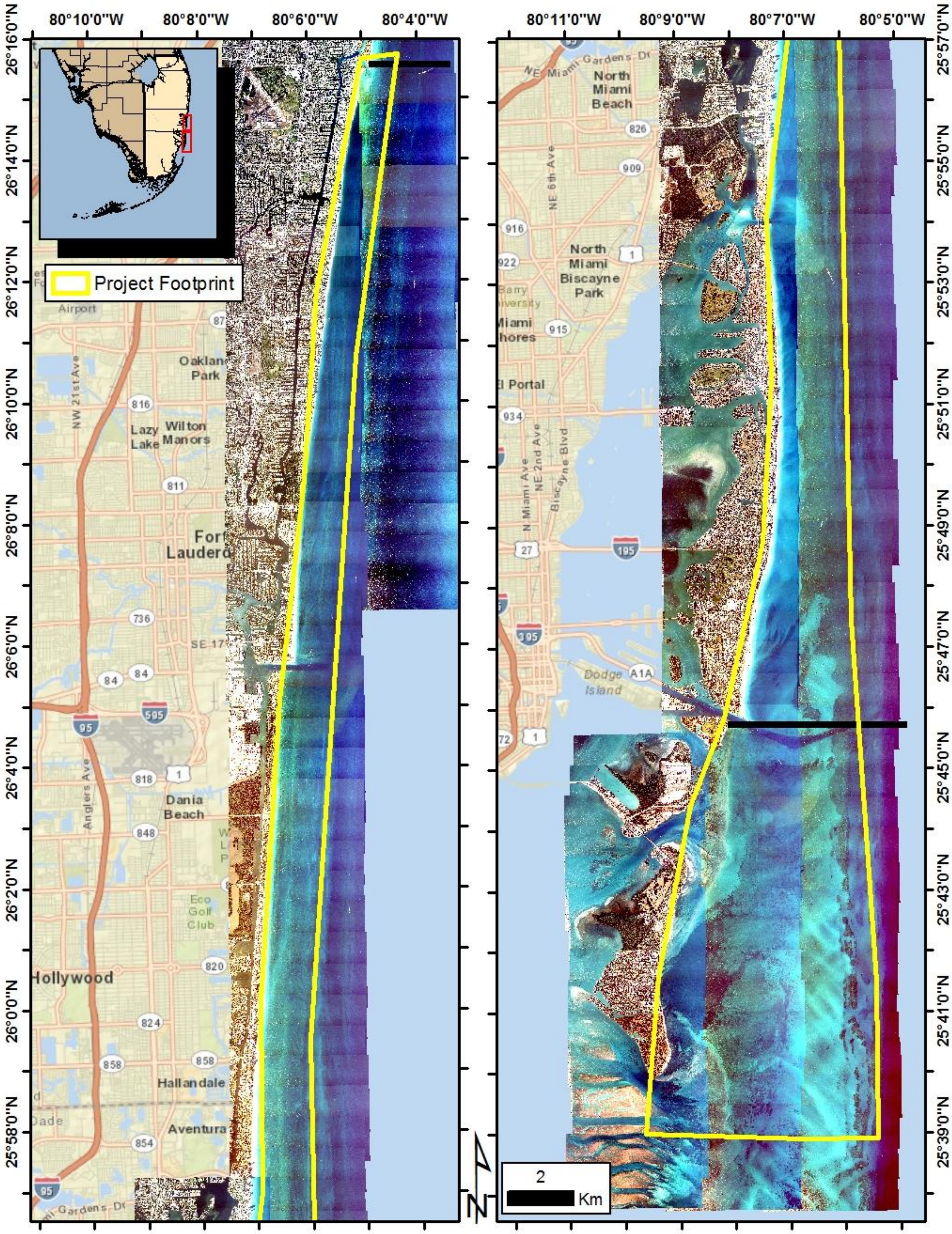


Figure 2. *Map of the 2013 aerial photographs taken for this project overlaying the ESRI street map layer.*

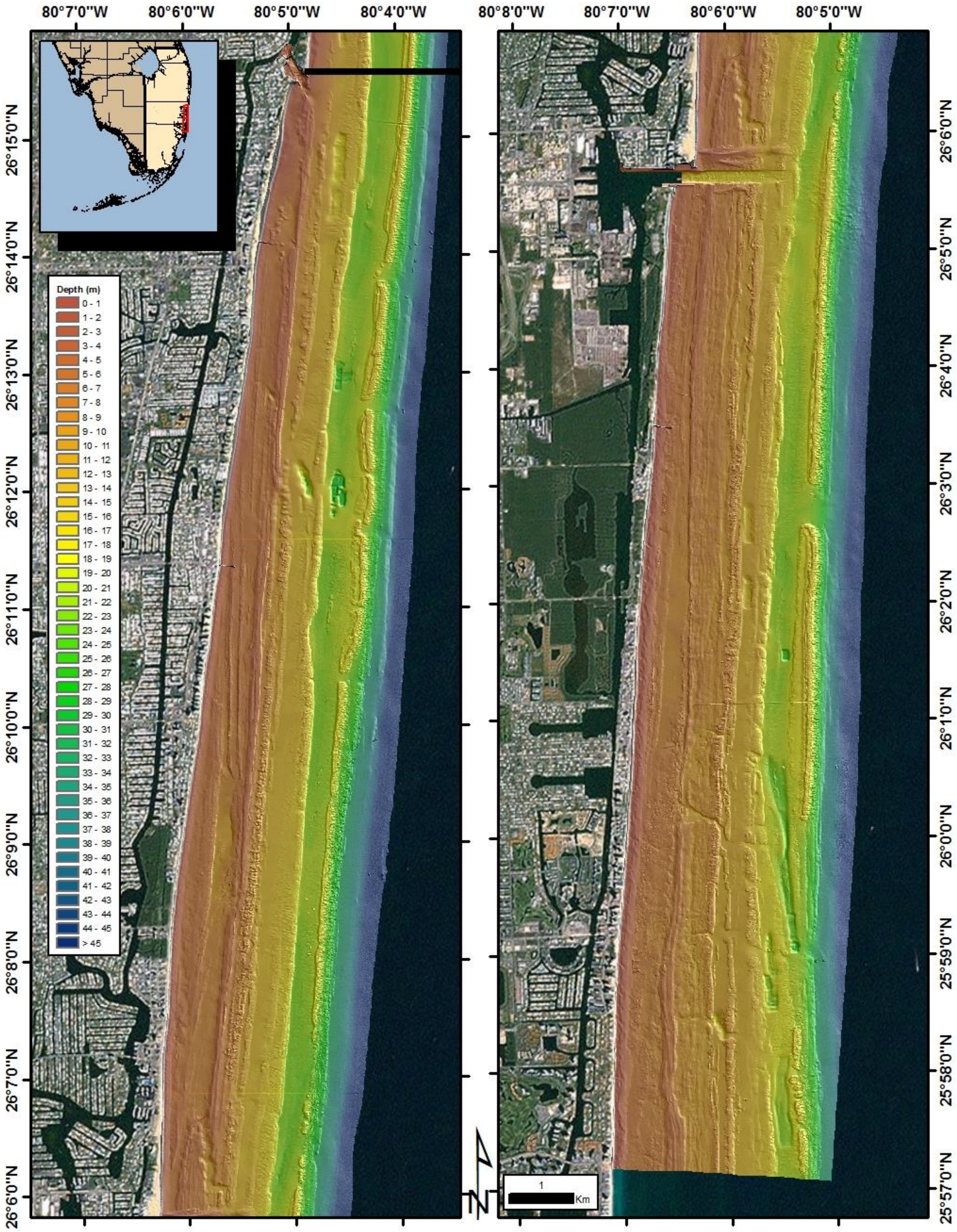


Figure 3. *Map of the 2008 LIDAR bathymetric survey for Broward County.*

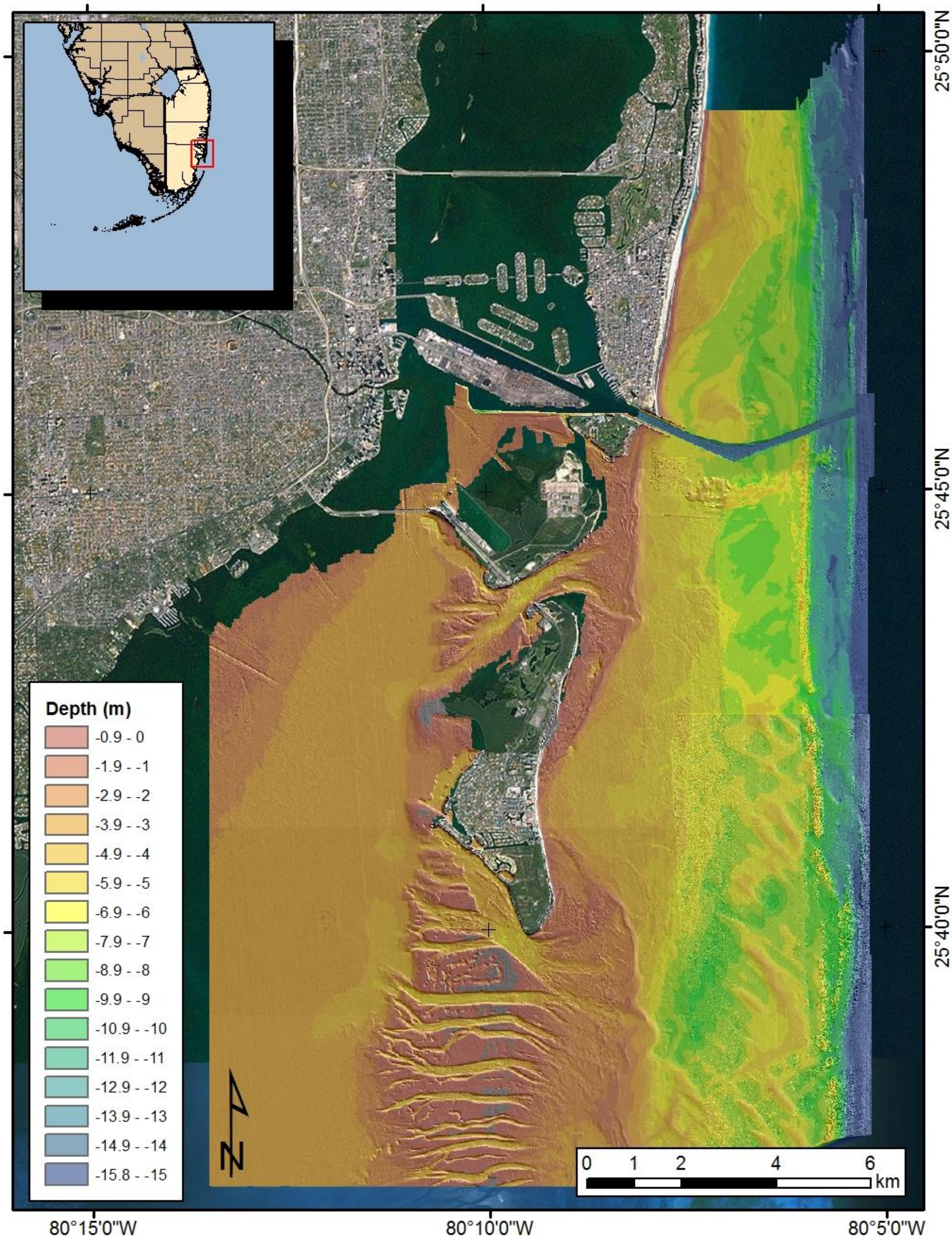


Figure 4. *Map of the 2009 NOAA OCS bathymetric survey for Miami-Dade County.*

3.3 Benthic Classification

Habitat polygons were drawn in ArcGIS using the remote data at a 1:1000 scale and a minimum mapping unit of 0.1 hectare. The final map polygons conformed to the previous southeast Florida mapping scheme (Walker *et al.* 2008; Walker 2009, 2012; Walker and Gilliam 2013), which were based on the NOAA hierarchical classification scheme used in Puerto Rico and the U.S. Virgin Islands NOAA Technical Memorandum National Ocean Service (NOS) National Centers for Coastal Ocean Science (NCCOS) Center for Coastal Monitoring & Assessment (CCMA) 152 (Kendall *et al.*, 2002) with some modification. Habitat classification criteria were defined by location, geomorphologic characteristics, and biologic communities.

Changes to the NOAA scheme included the addition of ridge and sand borrow area categories, a "Linear Reef" category in lieu of "Aggregate Reef", a depth component for many classes, and the inclusion and modification of two seagrass categories. "Linear Reef", a NOAA category used in previous southeastern Florida mapping, was retained as a better descriptor instead of the more recent NOAA "Aggregate Reef" category. As the Biscayne ecosystem region contained significant areas of seagrasses, two categories of seagrasses were used: Continuous and Discontinuous. Acoustic ground discrimination results from previous mapping included a depth component for the colonized pavement, ridge, aggregated patch reef, and sand classes to indicate that habitat on these features varied with water depth. Although all mapping for this project was shallow, these modifiers were retained for future integration into the larger-scale regional map. Definitions for all nearshore mapped habitats are as follows:

I. **Coral Reef and Hardbottom:** Hardened substrate of unspecified relief formed by the deposition of calcium carbonate by reef-building corals and other organisms (relict or ongoing) or existing as exposed bedrock.

A. Coral Reef and Colonized Hardbottom: Substrates formed by the deposition of calcium carbonate by reef-building corals and other organisms or existing as exposed bedrock. Habitats within this category have some colonization by live coral.

1. Dense *Acropora cervicornis*: Areas of semi-continuous *A. cervicornis* coverage, containing large thickets (>100 m²), small thickets (<100 m²), individual colonies, and small fragments, within close proximity to one another (<4 m).

2. Linear Reef: Linear coral formations oriented parallel to shore or the shelf edge and following the contours of the shore or shelf edge. Includes commonly used terms such as fore reef, fringing reef, and shelf-edge reef.

   a. Linear Reef-Inner: A distinct, relatively continuous, shore-parallel reef that consists of a rich coral reef community, which crests in approximately 8 m depth and supports immature reef formation growing atop antecedent shallow colonized pavement. Previous acoustic and biological data indicates a distinct benthic community.

3. **Patch Reef:** Coral formations isolated from other coral reef formations by sand, seagrass, or other habitats and with no organized structural axis relative to the contours of the shore or shelf edge. A surrounding halo of sand is often a distinguishing feature of this habitat type when it occurs adjacent to submerged vegetation.

   a. **Individual Patch Reef:** Distinctive single patch reefs equal to or larger than the minimum mapping unit (MMU).

4. **Aggregated Patch Reef:** Clustered patch reefs individually too small (smaller than the MMU) or too close together to map separately.

   a. **Aggregated Patch Reef-Shallow**: Clustered patch reefs individually too small (less than the MMU) or too close together to map separately in water depths <20 m.

5. **Scattered Coral/Rock in Unconsolidated Sediment:** Primarily sand bottom with scattered rocks too small to be delineated individually, in water shallower than 20 m.

6. **Colonized Pavement:** Flat, low-relief, solid carbonate rock with coverage of macroalgae, stony coral, gorgonians, and other sessile invertebrates dense enough to partially obscure the underlying carbonate rock.

   a. **Colonized Pavement-Shallow:** Colonized pavement in water shallower than 10 m. This category includes rubble in many areas; however, consolidated rubble fields are a less frequent feature in shallow water. Limited rubble and a wide, contiguous area of pavement occur, especially inshore of the ridge complexes. This area can have variable sand cover, which shifts in response to weather-induced wave energy. Thus, some of the colonized pavement will always be covered by shifting sand, and colonization density will be highly variable.

7. **Ridge:** Linear, shore-parallel, low-relief features that appear to be submerged cemented ancient shoreline deposits. They may be an extension of the foundation upon which the linear reefs grew further south and consist of early Holocene shoreline deposits; however, verification is needed. The biological cover is similar to that of colonized pavement, with macroalgae, scleractinians, gorgonians, and other sessile invertebrates dense enough to partially obscure the underlying carbonate rock.

    a. **Ridge-Shallow:** Linear, often shore-parallel, low-relief, geomorphologically distinct features in shallow water near shore. Their benthic cover remains similar to the shallow colonized pavement communities on the surrounding hard grounds. They presumably consist of early Holocene shoreline deposits with possibly some *Acropora* framestones. Verification is needed.

II. **Seagrass:** Habitat with 10 percent or more cover of *Thalassia testudinum* and/or *Syringodium filiforme*.

A. **Continuous Seagrass:** Seagrass community covering 90 percent or greater of the substrate. May include blowouts of less than 10 percent of the total area that are too small to be mapped independently (less than the MMU).

B. **Discontinuous Seagrass**: Seagrass community with breaks in coverage that are too diffuse, irregular, or result in isolated patches too small (smaller than the MMU) to be mapped as continuous seagrass.

III. **Unconsolidated Sediments:** Unconsolidated sediment with less than 10 percent cover of submerged vegetation.

A. **Sand:** Coarse sediment typically found in areas exposed to currents or wave energy.

1. **Sand–Shallow:** Shallow-water (<25 m) sediment exposed to a higher energy environment. Large, mobile sand pockets are found on the areas of consolidated hardgrounds. Sand movement is likely a deciding factor in the generation of benthic patterns in this habitat.

IV. Other Delineations:

A. **Artificial:** Manmade habitats such as submerged wrecks, large piers, submerged portions of rip-rap jetties, and the shoreline of islands created from dredge spoil.

B. **Inlet Channel:** All inlet channels in the survey area are maintained artificially and are characterized by dredged bottom and spoil ridges on their flanks.

C. **Sand Borrow Areas:** Several borrow pits from previous dredging projects are found throughout the survey area. Although they are all found in sandy areas, exposed limestone may be present that can harbor a strongly localized and patchy, but sometimes dense, benthic fauna.

3.4 Groundtruthing

In total, 265 groundtruthing locations identified in the remote data as needing field confirmation were visited to aid in feature identification (Figure 5). Researchers visited sites and either snorkeled the area around the point to identify the habitat at that location while collecting photos and short videos, or they used a Sea Viewer 950 underwater color video drop camera with a Sea-trak global positioning system (GPS) video overlay connected to a Garmin Wide Area Augmentation System (WAAS) GPS (~3 m accuracy). Color video was taken at each target location by dropping the camera over the side of a stationary/slowly drifting vessel approximately 0.5 – 2 m from the bottom. Video clips (15 sec to 2 min) were recorded directly to a digital video recorder in MPEG4 video format at 720x480 resolution and 30 frames sec^{-1}. Video length depended on habitat type and vessel drift. Videos of large expansive sand habitats were generally short, while reef habitats, especially edges, were longer. The GPS location at the start and end of each video were entered into a database and plotted in GIS. These data were also categorized according to major habitat type at each location. These data were then referenced to train the visual interpretation and correct the draft map of any false categorizations in the polygonal habitat layer.

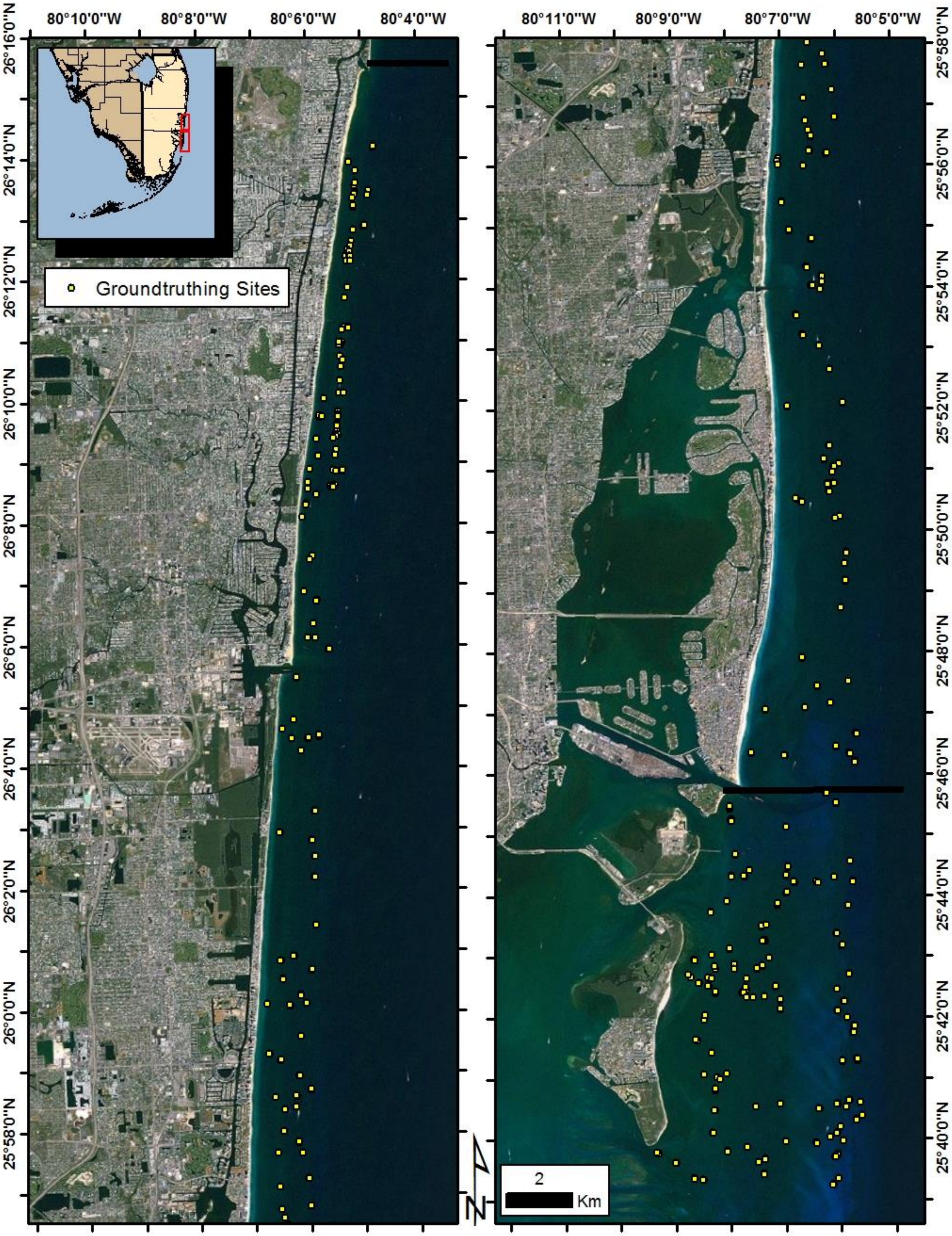


Figure 5. *Map of the 265 groundtruthing locations visited throughout the project area.*

3.5 Data Collection

Survey data were collected to provide a rigorous determination of habitat types, valuable information about the composition of the benthic communities for resource management, and data to statistically test cross-shelf and latitudinal community differences. All survey data were collected between April and June 2014. Five 1-km wide cross-shelf corridors were placed as evenly as possible across the mapped space while maintaining consistent habitat types and amounts between corridors and avoiding any major anthropogenic influences such as shipping channels and proximity to inlets and outfalls (Figure 6). Survey site locations were stratified across three main habitats within each corridor: Colonized Pavement, Ridge, and Inner Reef (Figure 7). Five sites were randomly placed in each habitat at a minimum of 40 m apart giving a total of 70 sites. Corridor 1 was the only corridor with two hardbottom habitats (Ridge habitat absent); all others had three.

Methodology for benthic assessments was adopted from established local methods for species' densities and sizes (Gilliam *et al.* 2010; Gilliam & Walker 2011; Walker & Gilliam 2013), those used in the Mesoamerican Barrier Reef System Project (Almada-Villela *et al.*, 2003) and the widely used Atlantic and Gulf Rapid Reef Assessment for percent cover (AGRRA, 2000). Data at each site were collected on four 20-m point-intercept transects at an intercept density of 0.2 m for a total of 400 (100 x 4) points per site. At each point, divers identified the organism under the transect tape by major functional groups (e.g., stony coral species, turf algae, macroalgae) or bare substrate type. In a 0.75-m wide belt (15 m^2 per transect) on one side of the four point intercept transects, divers recorded data on all stony corals greater than or equal to 4 cm in diameter, and all gorgonians greater than or equal to 4 cm in height. Species, colony size, percent mortality, condition (pale or bleached), and presence of disease were recorded for stony corals. Gorgonians were categorized by morphology (rod, plume, fan, whip) and counted in four size classes (4 - 10, 11 - 25, 26 - 50, and >50 cm). The presence of the sponge *Xestospongia muta* was counted, along with the number of stony coral colonies infected with *Cliona* spp. When a coral colony had multiple patches of *Cliona* spp., it would be counted as one sponge. The entire area surveyed was 4,200 m^2.

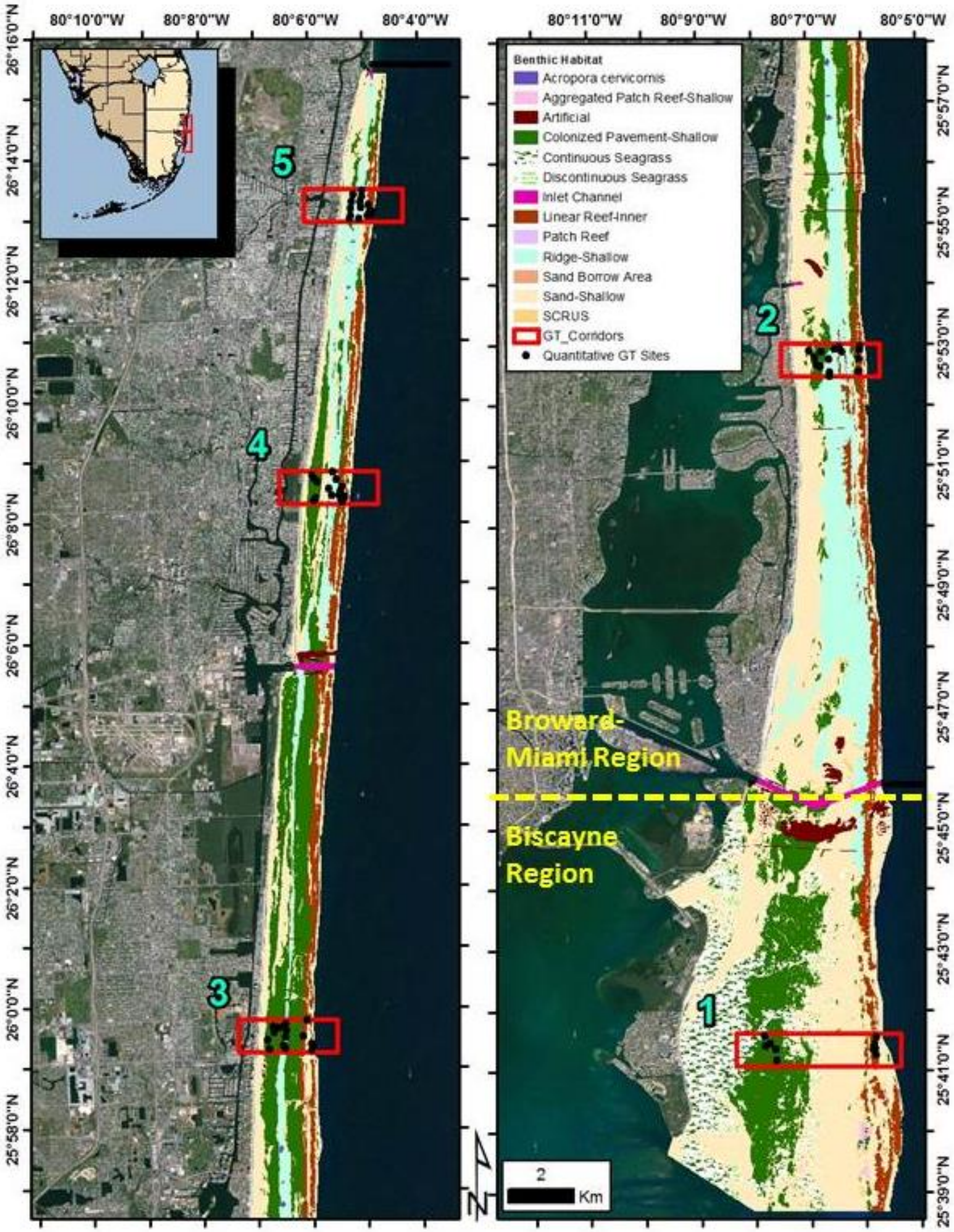


Figure 6. *Map of the 70 benthic survey locations within the five cross-shelf corridors overlaying the benthic habitat map and the ESRI Imagery base layer.*

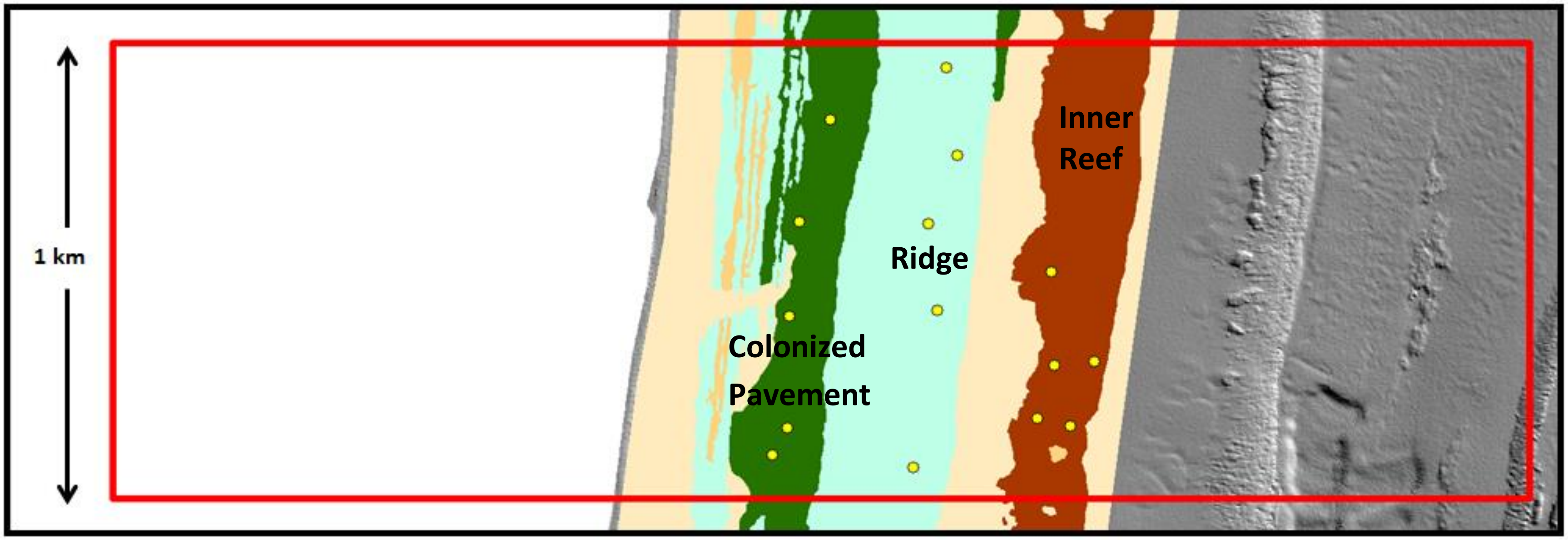


Figure 7. Example of a 1-km-wide cross-shelf corridor containing the three main habitat types: Colonized Pavement (green), Ridge (blue), and Inner Reef (brown), with 5 sites randomly placed >40 m apart within each hardbottom habitat type.

3.6 Statistical Analysis Methods

A cluster analysis and corresponding non-metric, multi-dimensional scaling (MDS) plot was constructed using Bray-Curtis similarity indices (PRIMER v6) of the percent benthic cover transect data (square-root transformed) to evaluate similarities between sites, where a shape represents a site. The sites were categorized by corridor and map habitat types *a priori* and entered in PRIMER as factors. The MDS plot was then configured to display the factors to illustrate the analyses' results. The MDS plot shows statistical similarities and differences in multivariate data by plotting them in two dimensions, where the relative distance apart is indicative of their similarity. Thus, sites very close together are more similar than those further apart, and the sites furthest apart are the least similar. These analyses were run between all sites within each corridor to evaluate local cross-shelf habitat differences and between all sites in a given habitat type to look at latitudinal community differences. ANOSIM tables depict where significant differences occur, while similarity percentages (SIMPER) analysis indicate what variables were responsible for driving these differences.

After the multi-dimensional scaling (MDS) plots were constructed using Bray-Curtis similarity indices (PRIMER v6) of the percent benthic cover transect data (square-root transformed), these plots were converted to 2D bubble plots. By selecting a specific variable, these plots visually illustrate the magnitude of percent cover for that variable at each particular site, as the area of the bubble is an indicator of the magnitude of percent cover for the particular substrate chosen. For all corridors and habitats, six bubble plots were created to represent six different substrates. Three of the bubble plots were created for stony corals, gorgonians, and unconsolidated sediment substrates in all corridors and habitats, while the remaining three bubble plots illustrate substrates that contributed most to the corridors and habitats splitting apart from one another.

Benthic quadrat transect data was untransformed and analyzed using nonparametric comparisons for each pair using the Wilcoxon signed-rank test.

4. RESULTS

4.1 Benthic Habitat Mapping

Of the 172.73 km² seafloor mapped, the polygon totals indicated 41.34% was Sand, 47.07% Coral Reef and Colonized Pavement, 9.35% Seagrass, and 2.25% Other Delineations (Table 1) (Figure 8). These totals are estimates due to some habitats having a substantial area of sand within. For example, the Scattered Coral/Rock in Sand (SCRUS) category, 1.62 km² of habitat, contained varying unknown ratios of sand to hardbottom. However, although this represented only 0.94% of the total area, such sand contributions slightly inflated the area summaries of hardbottom habitats. Therefore, the areas in Table 1 for Aggregated Patch Reef-Shallow, Scattered Coral Rock in Sand-Shallow, and Discontinuous Seagrass are overestimates.

Three habitat types dominated the mapped hardbottom area: Colonized Pavement (38.36 km²), Ridge-Shallow (25.52 km²), and Linear Reef-Inner (14.99 km²). These comprised 97% of the hardbottom habitats. SCRUS comprised 2% and Aggregated Patch Reef, Patch Reef, and dense *Acropora cervicornis* together made up 1% of the mapped hardbottom habitats. Seagrass accounted for 9.35% of the map and occurred solely south of Government Cut. Continuous Seagrass comprised 73.7% of the mapped seagrasses and Discontinuous comprised 26.3%. Sand comprised 41.34% of the map and Other Delineations accounted for 2.25%. Artificial habitats accounted for 66.7% of the Other Delineations, the largest of which were focused near Government Cut and Port Everglades.

Thirty-five dense locations of *A. cervicornis* were found on the Ridge habitat during the mapping portion of this project, only seven of which were previously reported (Walker and Klug 2014). These patches are some of the largest found within the continental United States. Area estimates of the 28 newly confirmed locations are approximately 110,000 m^2 (Walker and Klug 2014).

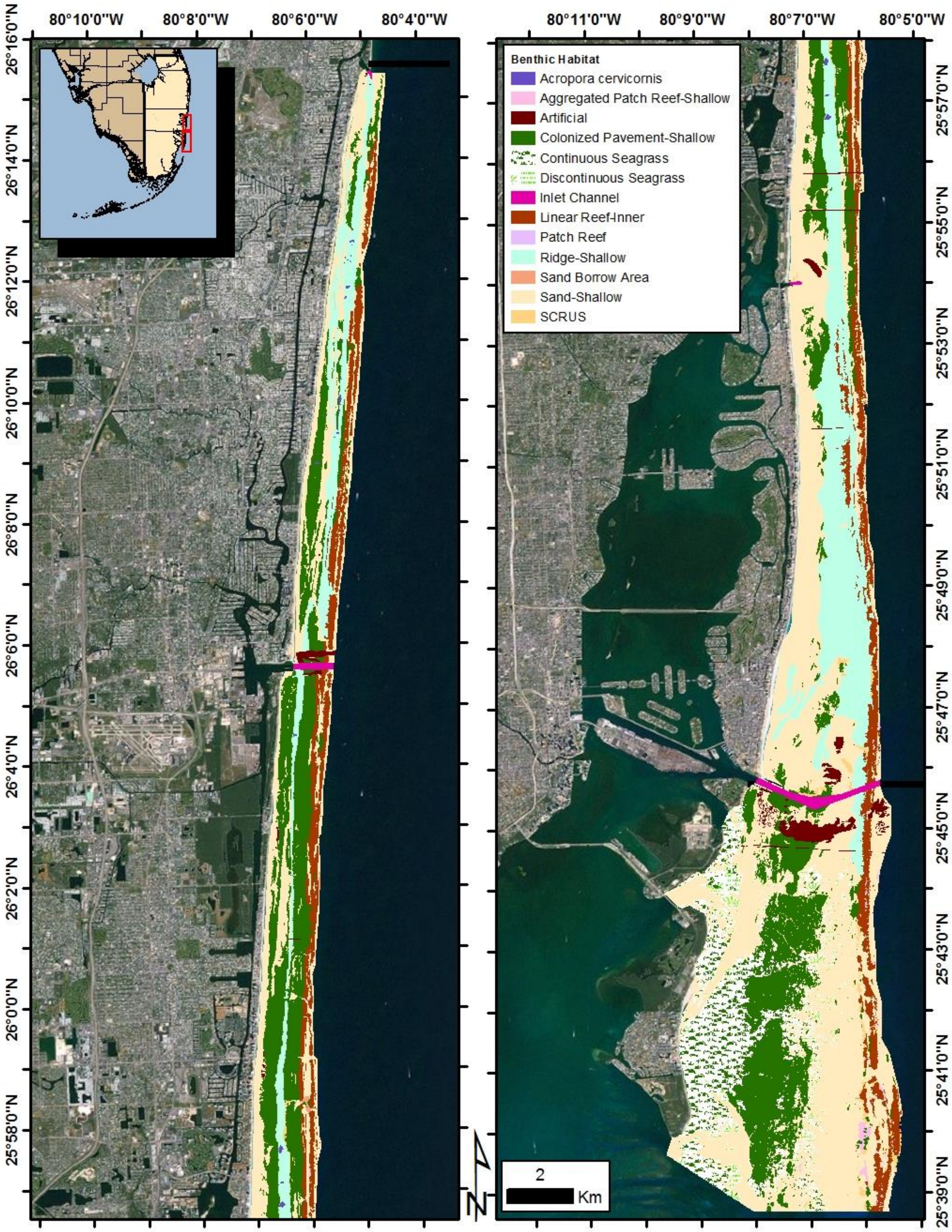


Figure 8. Map of the final benthic habitat map overlain the ESRI Imagery base layer.

Table 1. *Southeastern Florida nearshore benthic habitat polygon areas. Hierarchical habitats are nested within broader categories to the left. The total area in km^2 and the percent of the total mapped area are given for each category in all three hierarchical levels.*

SE FL Nearshore Benthic Habitat Areas (km^2) v3

Habitat	Type	Modifier	Modifier Area (km^2)	Habitat Area (km^2)
Coral Reef and Colonized Hardbottom	Acropora cervicornis		0.16 ; 0.09%	81.30 ; 47.07%
	Colonized Pavement	Shallow	38.36 ; 22.21%	
	Ridge	Shallow	25.52 ; 14.77%	
	Linear Reef	Inner	14.99 ; 8.68%	
	Aggregated Patch Reef	Shallow	0.64 ; 0.37%	
	Patch Reef	Shallow	0.013 ; 0.008%	
	Scattered Coral/Rock in Sand	Shallow	1.62 ; 0.94%	
Unconsolidated Sediment	Sand	Shallow	71.40 ; 41.34%	71.40 ; 41.34%
Seagrass	Seagrass	Continuous	11.89 ; 6.88%	16.14 ; 9.35%
		Discontinuous	4.25 ; 2.46%	
Other Delineations	Artificial		2.59 ; 1.50%	3.88 ; 2.25%
	Inlet Channel		1.17 ; 0.67%	
	Sand Borrow Area		0.13 ; 0.07%	
Total Mapped Area (km^2)			172.73 100.00%	172.73 ; 100.00%

4.2 Study-wide Coral, Gorgonian and Sponge Summaries

Quantitative data were collected on 4,568 stony coral colonies belonging to 22 species (Table 2). Total density was 1.09 corals/m^2. It is important to note that this density was not equal among all sites, habitats, and corridors.

Table 2. *List of stony coral species, abundance, and their percentage of the total corals observed in the benthic quadrat surveys, sorted by the most abundant.*

Species	Abundance	Percent
Porites astreoides	1356	29.68%
Siderastrea siderea	801	17.54%
Acropora cervicornis	471	10.31%
Porites porites	411	9.00%
Stephanocoenia intersepta	352	7.71%
Montastraea cavernosa	282	6.17%
Agaricia agaricites	233	5.10%
Dichocoenia stokesii	209	4.58%
Solenastrea bournoni	191	4.18%
Meandrina meandrites	101	2.21%
Pseudodiploria strigosa	39	0.85%
Orbicella faveolata	33	0.72%
Pseudodiploria clivosa	28	0.61%
Agaricia fragilis	26	0.57%
Colpophyllia natans	12	0.26%
Orbicella annularis	6	0.13%
Diploria labyrinthiformis	5	0.11%
Eusmilia fastigiata	4	0.09%
Madracis decactis	3	0.07%
Mycetophyllia aliciae	3	0.07%
Agaricia lamarcki	1	0.02%
Solenastrea hyades	1	0.02%
Total	**4568**	**100.00%**

Table 3. *Total stony coral density (colony/m^2) pooled for all sites by species, habitat and corridor.*

	Colonized Pavement					Total	Ridge				Total	Inner Reef					Total	Grand Total
Species	**1**	**2**	**3**	**4**	**5**		**2**	**3**	**4**	**5**		**1**	**2**	**3**	**4**	**5**		
Acropora cervicornis	0.000	0.000	0.187	0.597	0.000	0.157	0.157	0.293	0.253	0.000	0.176	0.000	0.077	0.000	0.007	0.000	0.017	0.112
Agaricia agaricites	0.000	0.003	0.000	0.000	0.000	0.001	0.000	0.000	0.013	0.003	0.004	0.620	0.027	0.007	0.063	0.040	0.151	0.055
Agaricia fragilis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.043	0.000	0.000	0.003	0.017	0.006
Agaricia lamarcki	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.001	0.000
Colpophyllia natans	0.000	0.003	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.017	0.007	0.003	0.000	0.010	0.007	0.003
Dichocoenia stokesii	0.007	0.043	0.047	0.013	0.000	0.022	0.047	0.047	0.030	0.043	0.042	0.163	0.050	0.037	0.113	0.057	0.084	0.050
Diploria labyrinthiformis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.001	0.007	0.000	0.003	0.000	0.003	0.003	0.001
Eusmilia fastigiata	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.003	0.001
Madracis decactis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.003	0.003	0.002	0.001
Meandrina meandrites	0.000	0.000	0.017	0.000	0.000	0.003	0.007	0.043	0.000	0.000	0.013	0.013	0.067	0.060	0.053	0.077	0.054	0.024
Montastraea cavernosa	0.003	0.000	0.030	0.053	0.000	0.017	0.040	0.083	0.113	0.007	0.061	0.007	0.110	0.217	0.167	0.110	0.122	0.067
Mycetophyllia aliciae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.003	0.000	0.002	0.001
Orbicella annularis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.010	0.007	0.004	0.001
Orbicella faveolata	0.000	0.000	0.000	0.003	0.000	0.001	0.000	0.000	0.007	0.000	0.002	0.070	0.003	0.010	0.010	0.007	0.020	0.008
Porites astreoides	0.000	0.020	0.263	0.180	0.000	0.093	0.090	0.787	0.140	0.057	0.268	1.287	0.410	0.187	0.937	0.163	0.597	0.323
Porites porites	0.027	0.263	0.023	0.013	0.143	0.094	0.033	0.120	0.027	0.067	0.062	0.260	0.050	0.040	0.220	0.083	0.131	0.098
Pseudodiploria clivosa	0.003	0.000	0.010	0.010	0.007	0.006	0.007	0.020	0.007	0.013	0.012	0.007	0.000	0.003	0.007	0.000	0.003	0.007
Pseudodiploria strigosa	0.003	0.000	0.007	0.007	0.000	0.003	0.007	0.003	0.000	0.000	0.003	0.060	0.013	0.003	0.010	0.017	0.021	0.009
Siderastrea siderea	0.037	0.037	0.077	0.103	0.117	0.074	0.073	0.107	0.117	0.163	0.115	0.597	0.400	0.250	0.347	0.247	0.368	0.191
Solenastrea bournoni	0.020	0.073	0.183	0.000	0.000	0.055	0.050	0.027	0.027	0.007	0.028	0.063	0.043	0.077	0.047	0.020	0.050	0.045
Solenastrea hyades	0.003	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Stephanocoenia intersepta	0.007	0.060	0.080	0.013	0.000	0.032	0.030	0.030	0.040	0.007	0.027	0.130	0.317	0.247	0.063	0.150	0.181	0.084
Grand Total	0.110	0.503	0.923	0.993	0.267	0.559	0.540	1.563	0.773	0.367	0.811	3.343	1.633	1.153	2.060	0.997	1.837	1.088

A total of 30,076 gorgonians were counted, classified by morphotype (fan, plume, rod, whip), and binned into four height classes: 4-10 cm, 11-25 cm, 26-50 cm, >50 cm (Table 3). Rods had the highest density, contributing 72% (21,624) of the total counted, followed by plumes at 24% (7,205) and fans at 4% (1,247). No whips were observed. Overall, the 11-25-cm height bin was most dense (13,954 colonies), followed by the smallest height bin (8,036), and the 26-50-cm (6,193). Gorgonians >50 cm tall were least dense (1,893).

Table 4. *Total gorgonian density (gorgonians/m^2) pooled for all sites by morphotype, habitat and corridor.*

	Corridor 1	**Corridor 2**	**Corridor 3**	**Corridor 4**	**Corridor 5**	**Grand Total**
Fan	**0.143**	**0.156**	**0.383**	**0.346**	**0.406**	**0.297**
Colonized Pavement	0.000	0.023	0.160	0.110	0.010	0.061
Ridge	N/A	0.347	0.850	0.273	0.733	0.551
Inner Reef	0.287	0.097	0.140	0.653	0.473	0.330
Plume	**3.163**	**1.784**	**2.253**	**0.769**	**1.090**	**1.715**
Colonized Pavement	1.573	2.497	1.813	0.317	0.053	1.251
Ridge	N/A	1.537	1.763	0.607	0.617	1.131
Inner Reef	4.753	1.320	3.183	1.383	2.600	2.648
Rod	**4.390**	**5.706**	**6.356**	**5.071**	**3.968**	**5.149**
Colonized Pavement	5.943	8.373	9.263	6.810	0.140	6.106
Ridge	N/A	7.127	6.320	5.293	7.670	6.603
Inner Reef	2.837	1.617	3.483	3.110	4.093	3.028
Grand Total	**7.697**	**7.646**	**8.992**	**6.186**	**5.463**	**7.161**

Totals of 262 *Xestospongia muta* (Table 5) and 144 coral colonies infected with *Cliona* spp. were counted (Table 6). It is important to note that abundances of both were not equal among all sites, habitats, and/or corridors.

Table 5. *Total* Xestospongia muta *density pooled for all sites by habitat and corridor.*

	Corridor					
	1	**2**	**3**	**4**	**5**	**Grand Total**
Colonized Pavement	0.000	0.000	0.000	0.020	0.000	0.004
Ridge	N/A	0.003	0.010	0.073	0.000	0.022
Inner Reef	0.030	0.230	0.170	0.130	0.207	0.153
Grand Total	**0.015**	**0.078**	**0.060**	**0.074**	**0.069**	**0.062**

Table 6 *Total density of the number of coral colonies infected with* Cliona *spp. pooled for all sites by habitat and corridor.*

	Corridor					
	1	**2**	**3**	**4**	**5**	**Grand Total**
Colonized Pavement	0.000	0.003	0.077	0.013	0.000	0.019
Ridge	N/A	0.033	0.010	0.020	0.000	0.016
Inner Reef	0.093	0.057	0.067	0.087	0.020	0.065
Grand Total	**0.047**	**0.031**	**0.051**	**0.040**	**0.007**	**0.034**

4.3 Habitat Analyses

4.3.1 Stony Coral Mean Density

Mean coral density (colony/m^2) was lowest on the Colonized Pavement sites ($\bar{x} = 0.56 \pm 0.15$ SEM), higher on the Ridge sites ($\bar{x} = 0.81 \pm 0.16$ SEM), and highest on the Inner Reef sites ($\bar{x} = 1.8 \pm 0.15$ SEM) (Figure 9). The Inner Reef habitat was significantly higher than both the Colonized Pavement and Ridge habitats (ANOVA, $p < 0.0001$).

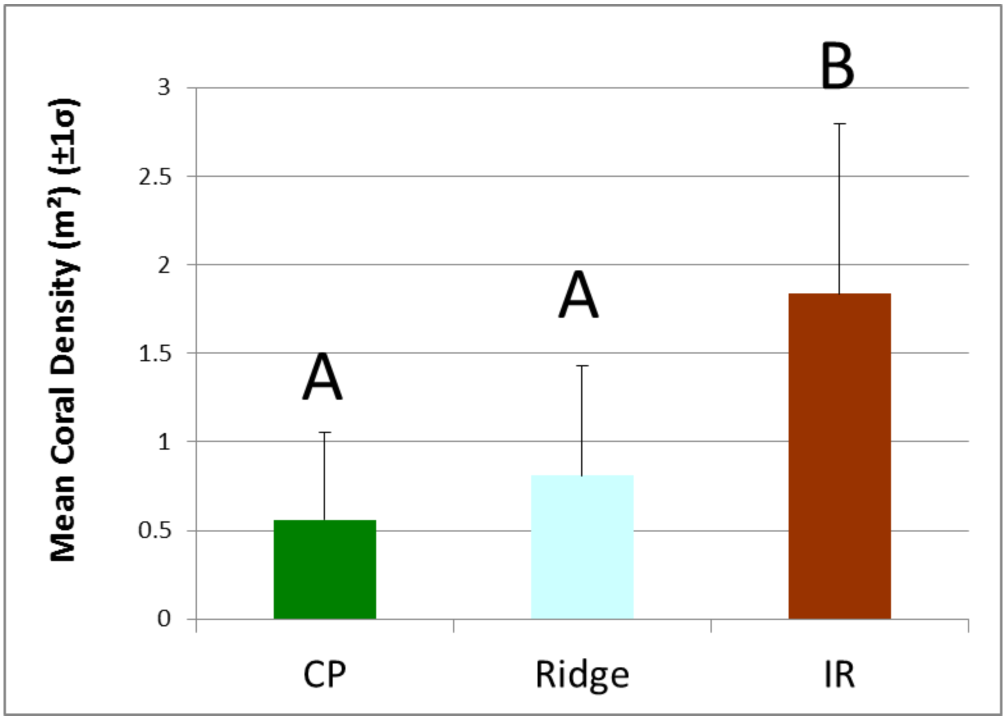


Figure 9. *Mean coral density by habitat. Error bars equal 1 standard deviation (σ). Letters denote significant differences.*

4.3.2 Stony Coral Mean Species Richness

As with coral density, the mean number of coral species (richness) varied by habitat, and all were significantly different from each other (Figure 10). Colonized Pavement had the lowest mean ($\bar{x} = 4.96 \pm 0.40$ SEM) (ANOVA, $p = 0.0006$), followed by the Ridge ($\bar{x} = 7.60 \pm 0.44$ SEM) (ANOVA, $p = 0.0006$), and the Inner Reef ($\bar{x} = 10.92 \pm 0.40$ SEM) (ANOVA, $p < 0.0001$), thus showing a cross-shelf increase away from shore.

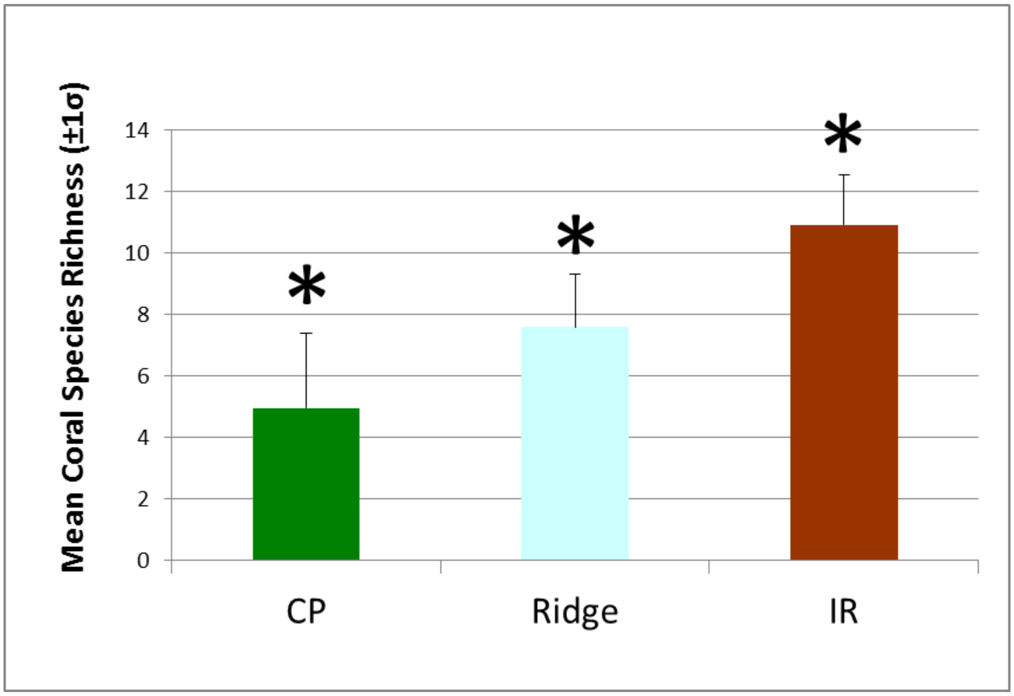


Figure 10. *Mean number of coral species by habitat. Error bars equal 1 standard deviation (σ). Asterisks denote significant differences.*

4.3.3 Gorgonian Mean Density by Habitat and Morphotype

Mean gorgonian density (gorgonian/m^2) varied by habitat and morphotype. Mean density on the Colonized Pavement habitat ($\bar{x}$ = 2.47 ± 0.36 SEM) differed significantly from that on both the Ridge ($\bar{x}$ = 2.76 ± 0.41 SEM) and Inner Reef ($\bar{x}$ = 2.00 ± 0.36 SEM) (ANOVA, p = 0.0303). In an analysis of gorgonian morphotypes combining all height classes (Figure 11), fans were least dense on the Colonized Pavement ($\bar{x}$ = 0.06 ± 0.52 SEM), densest on the Ridge ($\bar{x}$ = 0.55 ± 0.60 SEM), and occurred at an intermediate density on the Inner Reef ($\bar{x}$ = 0.33 ± 0.22 SEM). The fan morphotype density was significantly different on all habitat types (ANOVA, p = 0.0355). The plume morphotype was least dense on the Ridge ($\bar{x}$ = 1.13 ± 0.60 SEM), followed by Colonized Pavement ($\bar{x}$ = 1.25 ± 0.52 SEM), and densest on the Inner Reef ($\bar{x}$ = 2.65 ± 0.22 SEM). Plume density on the Inner Reef was significantly greater than both Colonized Pavement and Ridge (ANOVA, p = 0.0002). Rods were denser on all habitat types than both fans and plumes. However, unlike fans and plumes, rods were least dense on the Inner Reef ($\bar{x}$ = 3.03 ± 0.22 SEM), denser on the Colonized Pavement ($\bar{x}$ = 6.11 ± 0.52 SEM), and densest on the Ridge habitat ($\bar{x}$ = 6.60 ± 0.60 SEM). Rod densities on the Inner Reef were significantly lower than on both Colonized Pavement and Ridge (ANOVA, p = 0.0050).

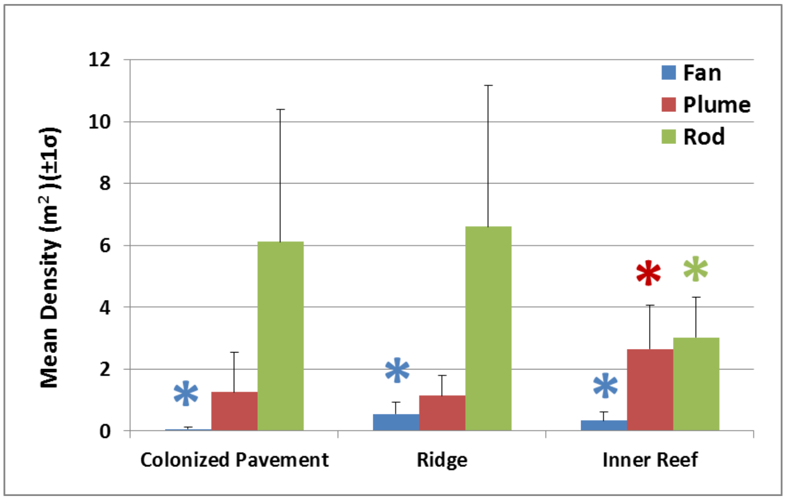


Figure 11. *Mean gorgonian density by habitat and morphotype. Error bars equal 1 standard deviation (σ). Asterisks denote significant differences by morphotype between habitats.*

4.3.4 Gorgonian Mean Density by Size Class, Habitat and Morphotype

Figure 12 illustrates gorgonian data by height class and habitat, and includes morphotype. Fan mean densities were lowest on Colonized Pavement and highest on the Ridge habitat, in all 4 size classes. Plume mean densities were highest on the Inner Reef for all size classes, lowest on the Colonized Pavement for the 4-10-cm and 11-25-cm height classes, and lowest on the Ridge for the 26-50-cm and >50 cm classes. Rod mean densities were highest on the Ridge habitat and lowest on the Inner Reef habitat for the 4-10 cm, 11-25 cm, and 26-50 cm classes. Rods >50 cm were most dense on the Colonized Pavement, and least dense on the Inner Reef.

4 – 10 cm: On the Colonized Pavement, fan density was significantly lower than on both the Ridge and Inner Reef (ANOVA, $p = 0.0001$). Plume density was significantly higher on the Inner Reef and increased with depth (ANOVA, $p = 0.0129$). Rod density was significantly greater on the Ridge than on the Inner Reef (ANOVA, $p = 0.0098$).

11 – 25 cm: Fan densities differed significantly among all habitat types (ANOVA, $p = 0.0045$). Plume density was significantly greater on the Inner Reef than in either other habitat and increased with depth (ANOVA, $p < 0.0001$). Rod density was also significantly greater on the Inner Reef than in either other habitat (ANOVA, $p = 0.0101$).

26 – 50 cm: Fan densities differed significantly among all habitat types (ANOVA, $p = 0.0353$). Plume density was significantly greater on the Inner Reef than on the Ridge (ANOVA, $p = 0.0048$). Rod density was significantly lower on the Inner Reef than in either other habitat (ANOVA, $p = 0.0011$).

>50 cm: Fan density was significantly lower on the Colonized Pavement than on either other habitat (ANOVA, $p = 0.0070$). Plume density was significantly higher on the Inner Reef than in either other habitat (ANOVA, $p = 0.0211$). Rod density was significantly lower on the Inner Reef than in either other habitat (ANOVA, $p = 0.0030$)

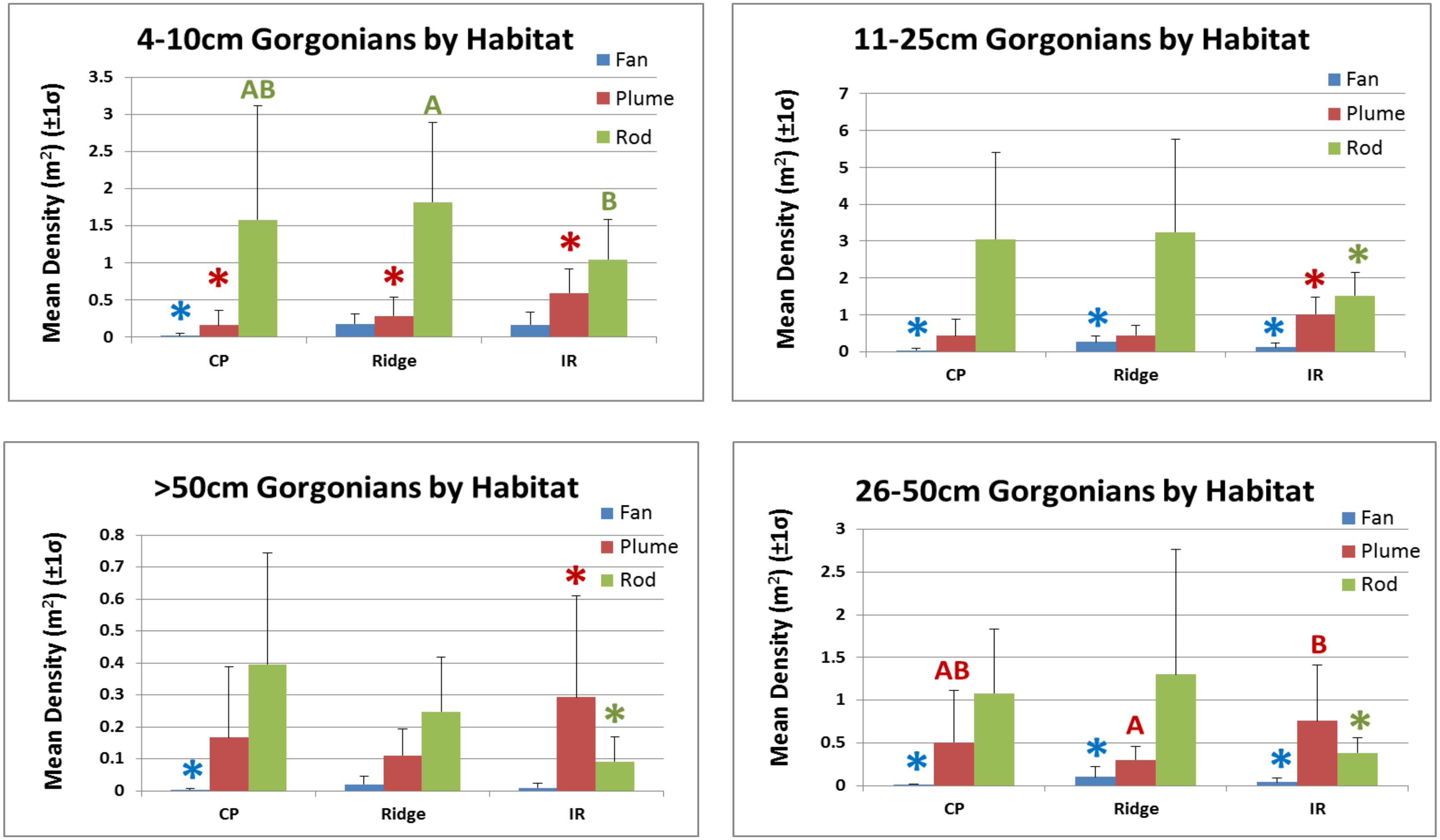


Figure 12. *Graphs for each gorgonian height class illustrating mean density by habitat and morphotype. Error bars equal 1 standard deviation (σ). Asterisks and letters denote significant differences by morphotype among habitats.*

4.3.5 Mean Sponge Density - *Xestospongia muta* and *Cliona* spp.

As with coral density and coral richness, *Xestospongia muta* density also increased across the shelf, beginning with the Colonized Pavement habitat (x̄ = 0.004 ± 0.02 SEM), through the Ridge habitat (x̄ = 0.02 ± 0.02 SEM) to the Inner Reef habitat (x̄ = 0.15 ± 0.02 SEM) (Figure 13), with density in the latter habitat significantly greater than either of the more inshore habitats (ANOVA, $p < 0.0001$). Of the 262 counted, 230 (87.7%) occurred at Inner Reef sites. Densities were lower than gorgonians and stony corals throughout the study.

By contrast, the number of coral colonies infected with *Cliona* spp. exhibited no cross-shelf increase (Figure 13). Although, as with coral density and richness, and *X. muta* density, *Cliona* spp. density was highest on the Inner Reef (x̄ = 0.06 ± 0.009 SEM), it was higher on the Colonized Pavement (x̄ = 0.019 ± 0.009 SEM) than on the Ridge (x̄ = 0.016 ± 0.01 SEM). Density on the Inner Reef was significantly greater than on both the Colonized Pavement and Ridge habitats (ANOVA, $p = 0.0002$). Of the 144 counted, 97 (67.4%) were found at Inner Reef sites.

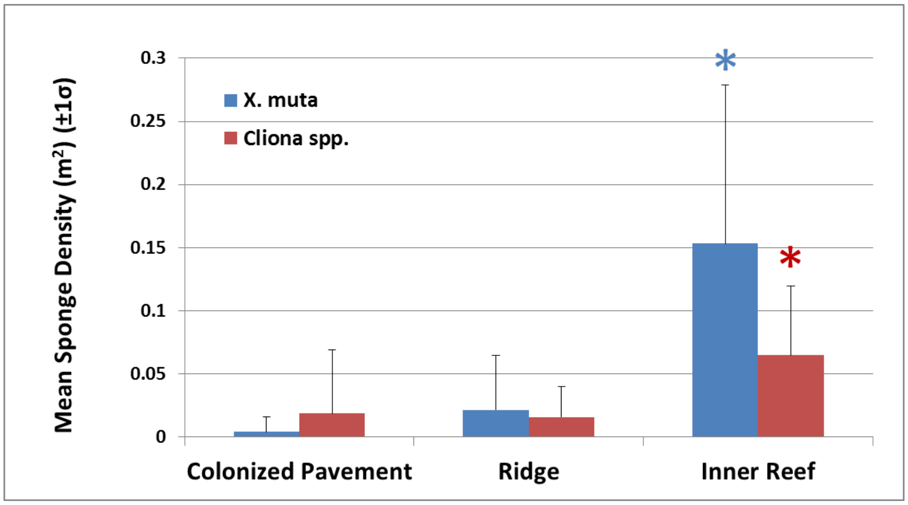
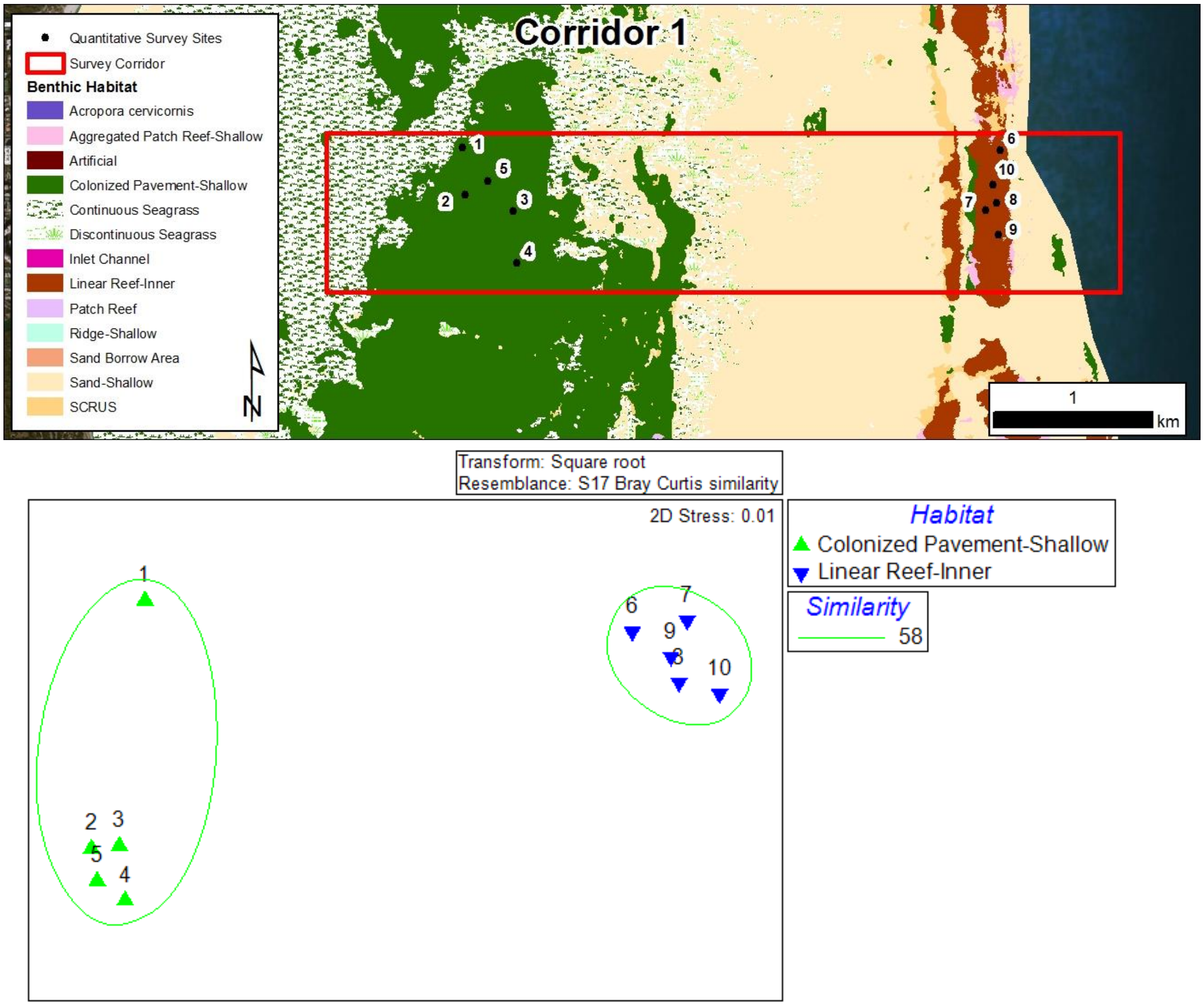


Figure 13. *Mean sponge density by habitat. Error bars equal 1 standard deviation (σ). Asterisks denote significant differences by sponge between habitats.*

4.3.6 Corridor 1 – Benthic Cover

All corridors exhibited significant differences in percent benthic cover between habitat types, yet some differences were stronger than others. In Corridor 1, the MDS plot and ANOSIM table (Figure 14) illustrate the clear distinction between Colonized Pavement and Inner Reef, the only two habitats present. The Ridge Complex does not extend this far south. A similarity percentages (SIMPER) analysis (based on square-root transformed data) showed that the two main factors driving these differences were the percentages of turf algae and macroalgae. The Inner Reef supported a higher percentage of turf algae ($\bar{x}$ = 48.95% ± 2.05 SEM) than the Colonized Pavement ($\bar{x}$ = 23.25% ± 3.29 SEM), whereas the Colonized Pavement sites exhibited a higher percentage of macroalgae ($\bar{x}$ = 35.45% ± 1.93 SEM) than on the Inner Reef sites ($\bar{x}$ = 10.00% ± 1.33 SEM). The Colonized Pavement sites also exhibited a high percentage of seagrass ($\bar{x}$ = 19.40 ± 5.53 SEM), which was absent on the Inner Reef sites, whereas the Inner Reef had a higher percentage of gorgonians ($\bar{x}$ = 20.35% ± 2.44 SEM) than the Colonized Pavement ($\bar{x}$ = 6.85% ± 1.04 SEM). MDS bubble plots (Figure 15) illustrate these differences.



ANOSIM Pairwise Test	**R Statistic**	**Significance Level %**
Habitat comparison		
Linear Reef-Inner, Colonized Pavement-Shallow	**1**	**0.8**

Figure 14. *Corridor 1 multivariate analyses results. Top: map showing randomly stratified survey locations. Middle: MDS plot of the Bray-Curtis similarity matrix of percent benthic cover data. Outlines represent 58% similarity from the cluster analysis. Bottom: tabular summary of the analysis of similarity (ANOSIM) pairwise test between habitat types. The closer the R statistic is to 1, the stronger the dissimilarity between groups. Bold indicates a significant result.*

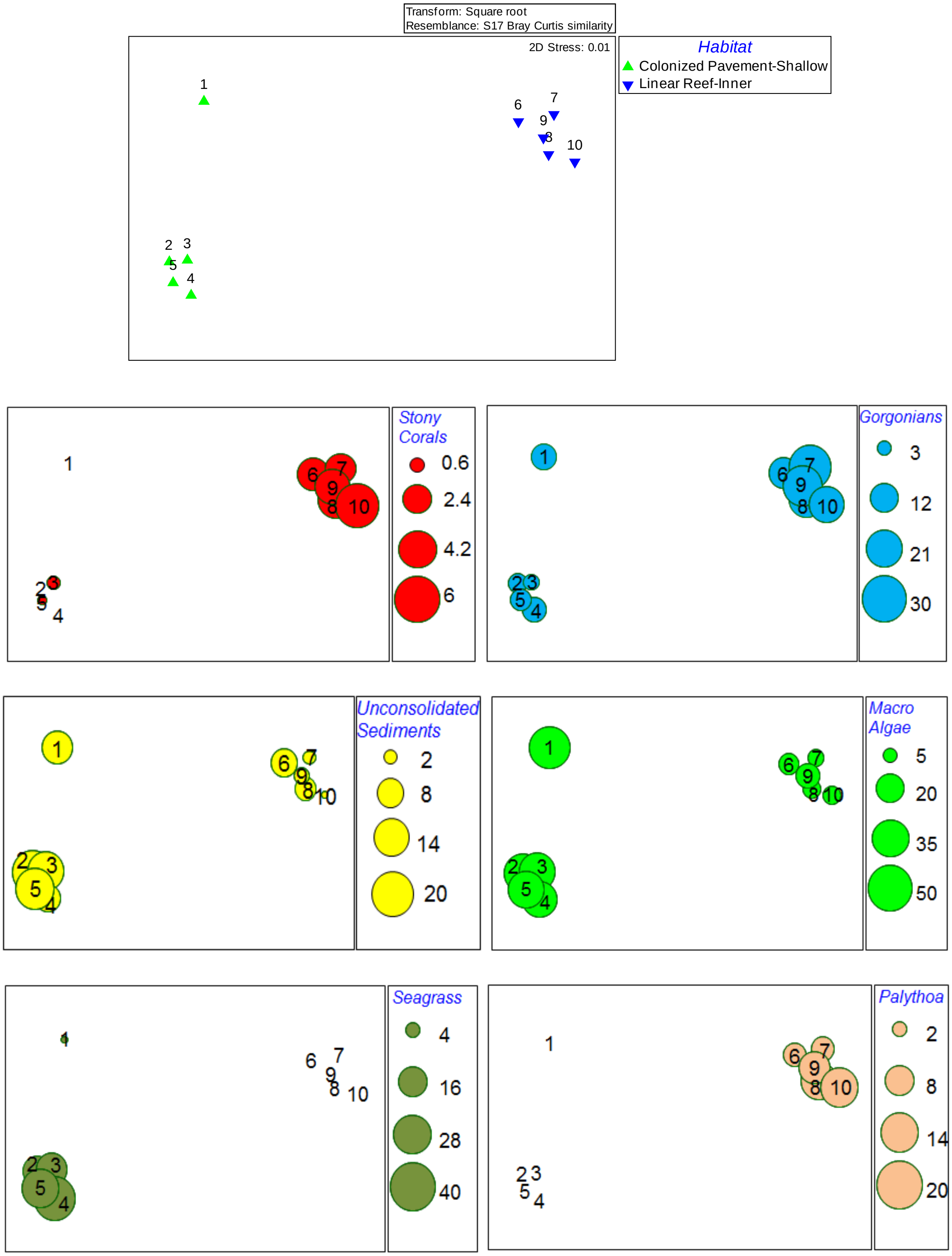


***Figure 15**. Corridor 1 corresponding 2D bubble plots.*

Figure 16 represents mean percent benthic cover comparisons for Corridor 1 based on untransformed data. The Colonized Pavement had significantly higher mean benthic cover values for macroalgae (ANOVA, p = 0.0122) and seagrass (ANOVA, p = 0.0075). The Inner Reef habitat had significantly higher mean benthic cover values for gorgonians (ANOVA, p = 0.0122) and stony corals (ANOVA, p = 0.0112).

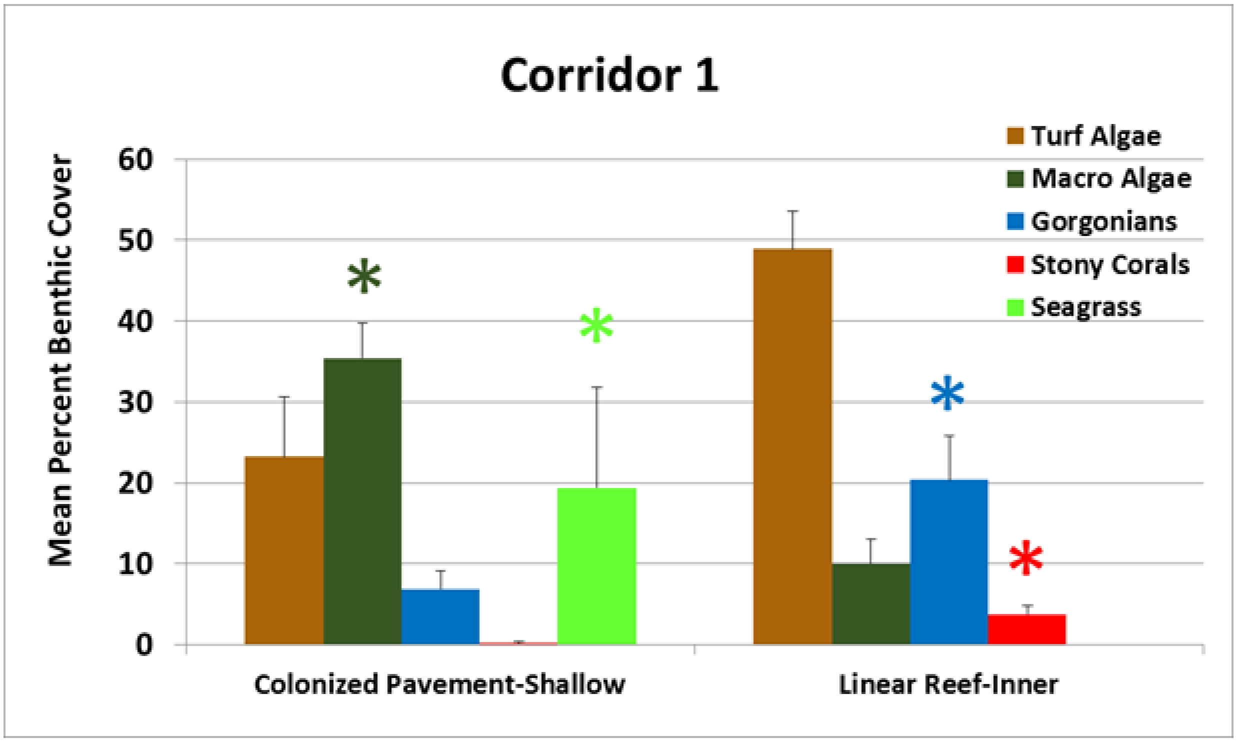
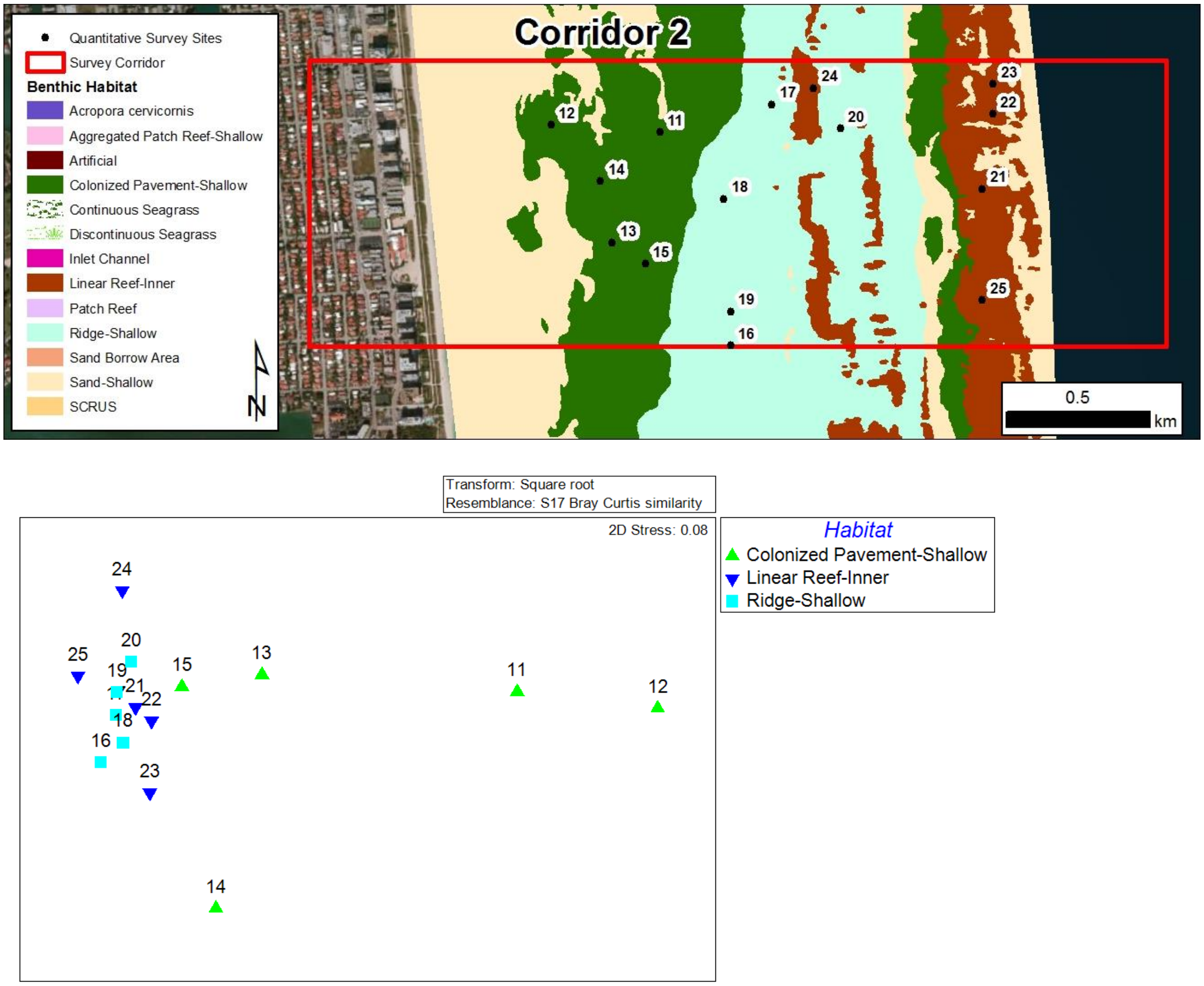


Figure 16. *Mean percent benthic cover for Corridor 1 by habitat. Error bars equal 1 standard deviation (σ). Asterisk denotes significant differences between functional groups.*

4.3.7 Corridor 2 – Benthic Cover

Mixed clustering in the MDS plot of Corridor 2 sites illustrates much weaker differences between habitat types (Figure 17), although Colonized Pavement sites were significantly different from Inner Reef and Ridge sites, due chiefly to the high percentage of sand on the Colonized Pavement ($\bar{x}$ = 20.50% ± 7.17 SEM) versus the Inner Reef ($\bar{x}$ = 4.25% ± 0.97 SEM) and Ridge ($\bar{x}$ = 3.05% ± 0.38 SEM) (SIMPER analysis based on square-root transformed data). The Colonized Pavement sites also had a lower percentage of turf algae cover ($\bar{x}$ = 46.90% ± 11.08 SEM) and a higher percentage of macroalgae ($\bar{x}$ = 16.95% ± 5.94 SEM), than the Inner Reef and Ridge sites, both of which had higher percentages of turf algae ($\bar{x}$ = 65.9% ± 3.07 SEM and $\bar{x}$=71.30% ±2.34 SEM, respectively) and lower percentages of macroalgae ($\bar{x}$ = 5.70% ± 0.95 SEM and $\bar{x}$ = 5.4% ± 0.56 SEM, respectively). These analyses revealed no measurable differences in patterns of percent cover between Inner Reef and Ridge sites, as reflected by the similar percentages for gorgonians, macroalgae, turf algae, and unconsolidated sediment (Figure 19). Sponge and stony coral cover was highest on the Inner Reef, and macroalgae cover was highest on Colonized Pavement sites. MDS bubble plots (Figure 18) illustrate these differences.



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Habitat comparison		
Colonized Pavement-Shallow, Linear Reef-Inner	**0.332**	**2.4**
Colonized Pavement-Shallow, Ridge-Shallow	**0.408**	**0.8**
Linear Reef-Inner, Ridge-Shallow	0.216	6.3

Figure 17. *Corridor 2 multivariate analyses results. Top: map showing randomly stratified survey locations. Middle: MDS plot of the Bray-Curtis similarity matrix of percent benthic cover data. Bottom: tabular summary of analysis of similarity (ANOSIM) pairwise test between habitat types. Data treatment as in Figure 14.*

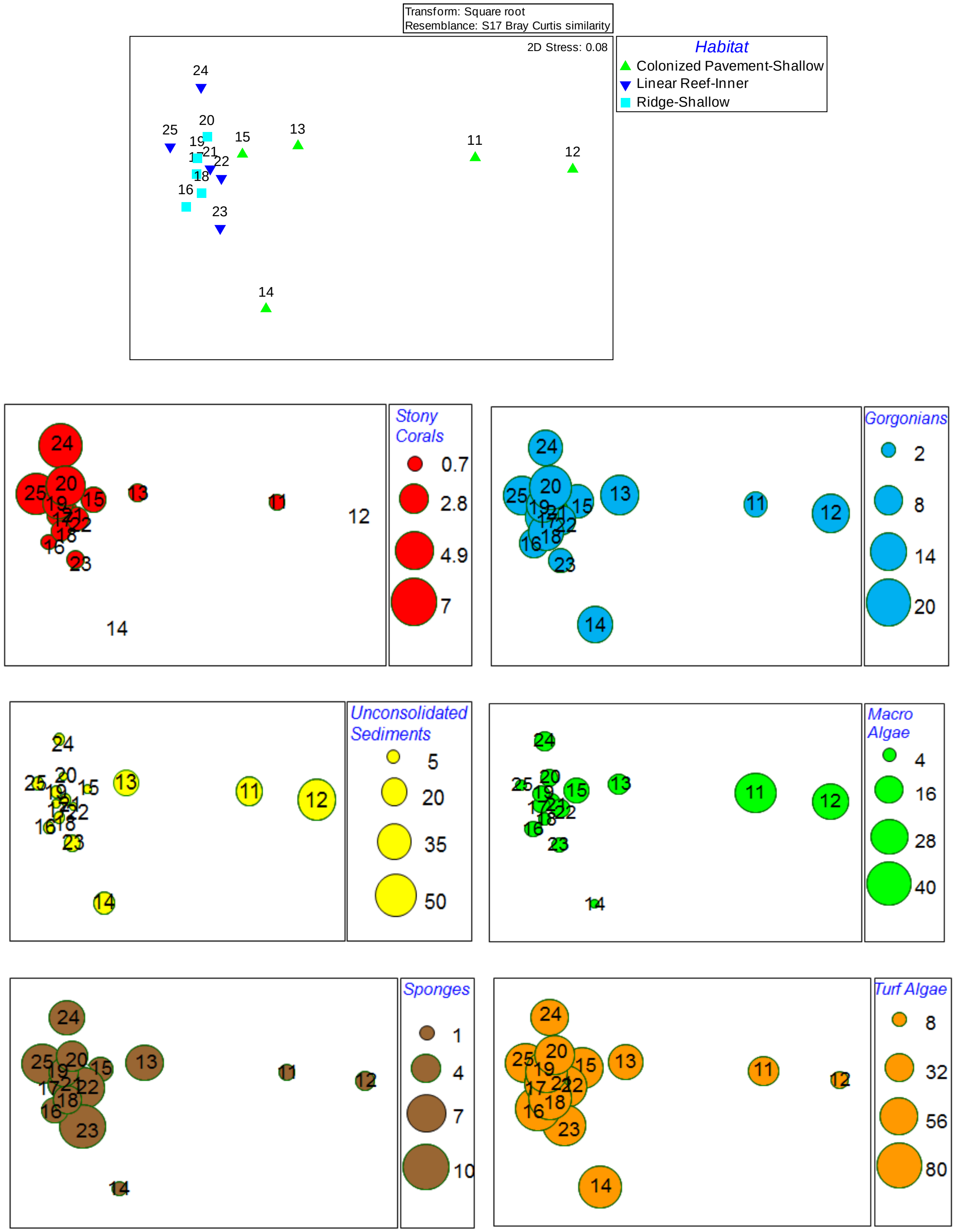


Figure 18. *Corridor 2 corresponding 2D bubble plots.*

Figure 19 represents mean percent benthic cover comparisons for Corridor 2 based on untransformed data. No significant differences of mean percent benthic cover in the functional groups listed below were found between habitat types, although many came close. For instance, turf algae on the Ridge was almost significantly higher than on the Colonized Pavement (ANOVA, p = 0.0601); stony coral cover on the Inner Reef was almost significantly higher than on the Colonized Pavement (ANOVA, p = 0.0740), and unconsolidated sediments on the Colonized Pavement almost accounted for significantly greater cover than on the Inner Reef (ANOVA, p = 0.0937).

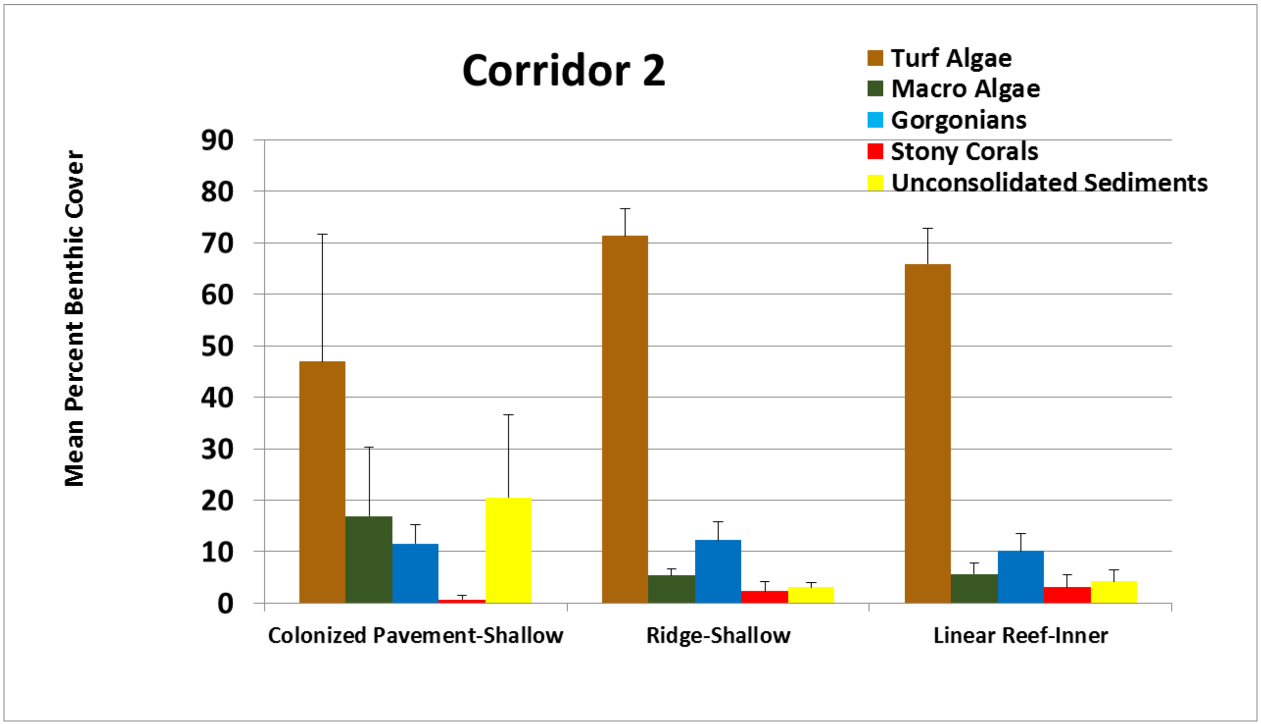
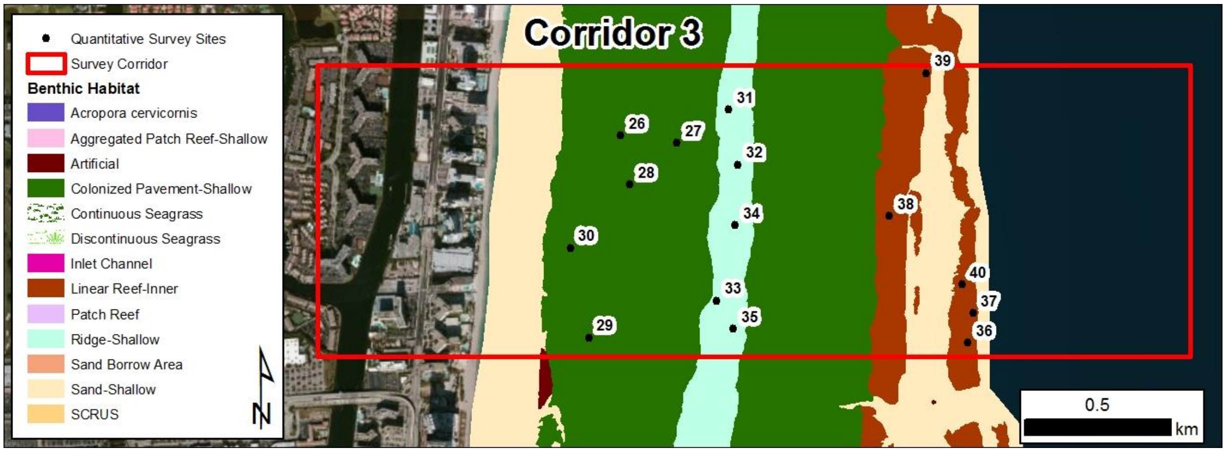
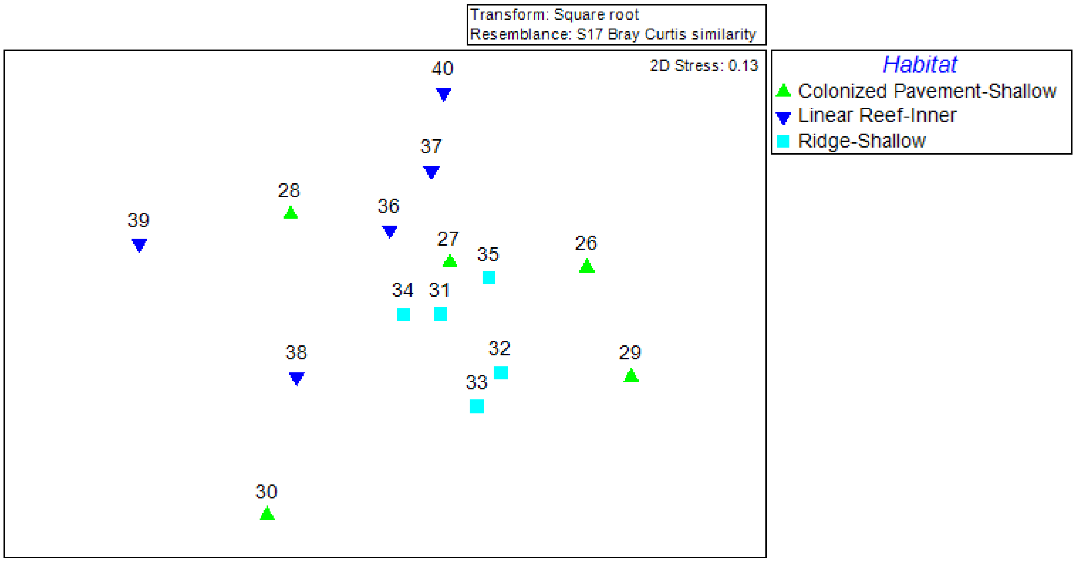


Figure 19. *Mean percent benthic cover for Corridor 2 by habitat. Error bars equal 1 standard deviation (σ).*

4.3.8 Corridor 3 – Benthic Cover

In Corridor 3, patterns of percent cover differ significantly between the Ridge sites relative to both Colonized Pavement and Inner Reef (ANOSIM) (Figure 20). Inner Reef and Ridge sites clustered separately in the MDS, while Colonized Pavement sites were scattered throughout, due mainly to the high percentage of stony corals on the Ridge ($\bar{x}$ = 4.05% ± 0.92 SEM), particularly *Acropora cervicornis*, which was found at all 5 sites (SIMPER based on square-root transformed data). The Inner Reef sites still had a relatively high percentage of stony corals ($\bar{x}$ = 2.9% ± 0.63 SEM), although *A. cervicornis* was absent. The Colonized Pavement sites had the lowest stony coral percentage ($\bar{x}$ = 1.95% ± 0.55 SEM), although *A. cervicornis* was found at 4 of the 5 sites. *Palythoa* spp. cover was also highest on the Ridge ($\bar{x}$ = 5.50% ± 0.67 SEM) relative to the Inner Reef ($\bar{x}$ = 1.65% ± 0.54 SEM) and Colonized Pavement ($\bar{x}$ = 4.15% ± 1.05 SEM). By contrast, macroalgae cover was highest on the Colonized Pavement ($\bar{x}$ = 15.60% ± 3.17 SEM), lowest on the Inner Reef ($\bar{x}$ = 9.95% ± 2.34 SEM), and intermediate on the Ridge ($\bar{x}$ = 12.65% ± 0.85 SEM). The MDS bubble plots further illustrate that the Inner Reef had the greatest cover of sponges and unconsolidated sediment, while the Colonized Pavement a high percentage cover of macroalgae (Figure 21). The broad spread of Colonized Pavement sites in the MDS plot reflects the greater variability of this habitat than the others.





ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Habitat comparison		
Colonized Pavement-Shallow, Linear Reef-Inner	0.18	9.5
Colonized Pavement-Shallow, Ridge-Shallow	**0.184**	**2.4**
Linear Reef-Inner, Ridge-Shallow	**0.436**	**0.8**

Figure 20. *Corridor 3 multivariate analyses results. Top: map showing randomly stratified survey locations. Middle: MDS plot of the Bray-Curtis similarity matrix of percent benthic cover data. Bottom: tabular summary of analysis of similarity (ANOSIM) pairwise test between habitat types. Data treatment as in Figure 14.*

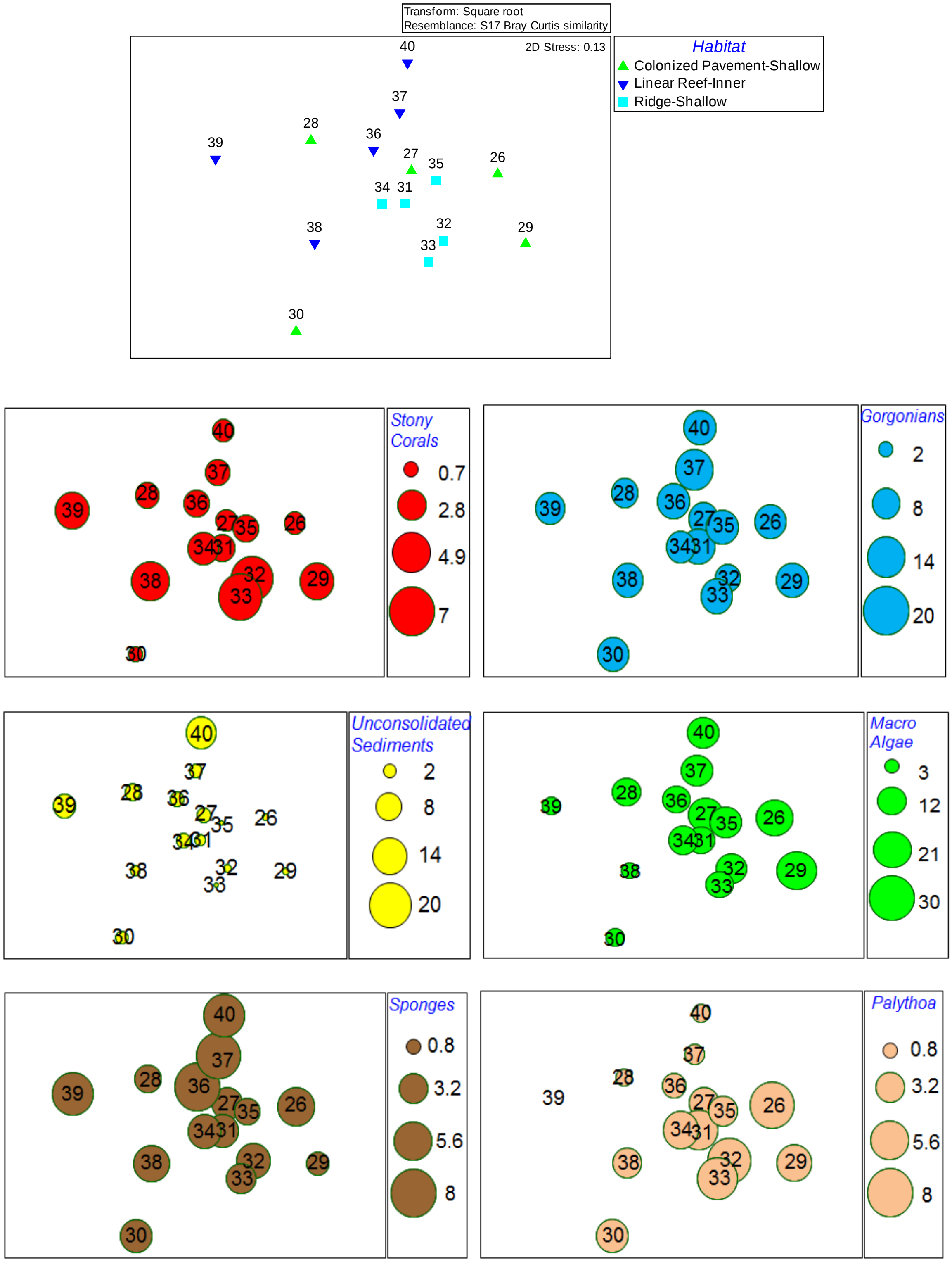


Figure 21*. Corridor 3 corresponding 2D bubble plots*

Figure 22 represents mean percent benthic cover comparisons for Corridor 3 based on untransformed data. *Palythoa* spp. exhibited the only significant difference of any functional group between habitats; it accounted for significantly greater mean cover on the Ridge habitat than on the Inner Reef (ANOVA, p = 0.0160).

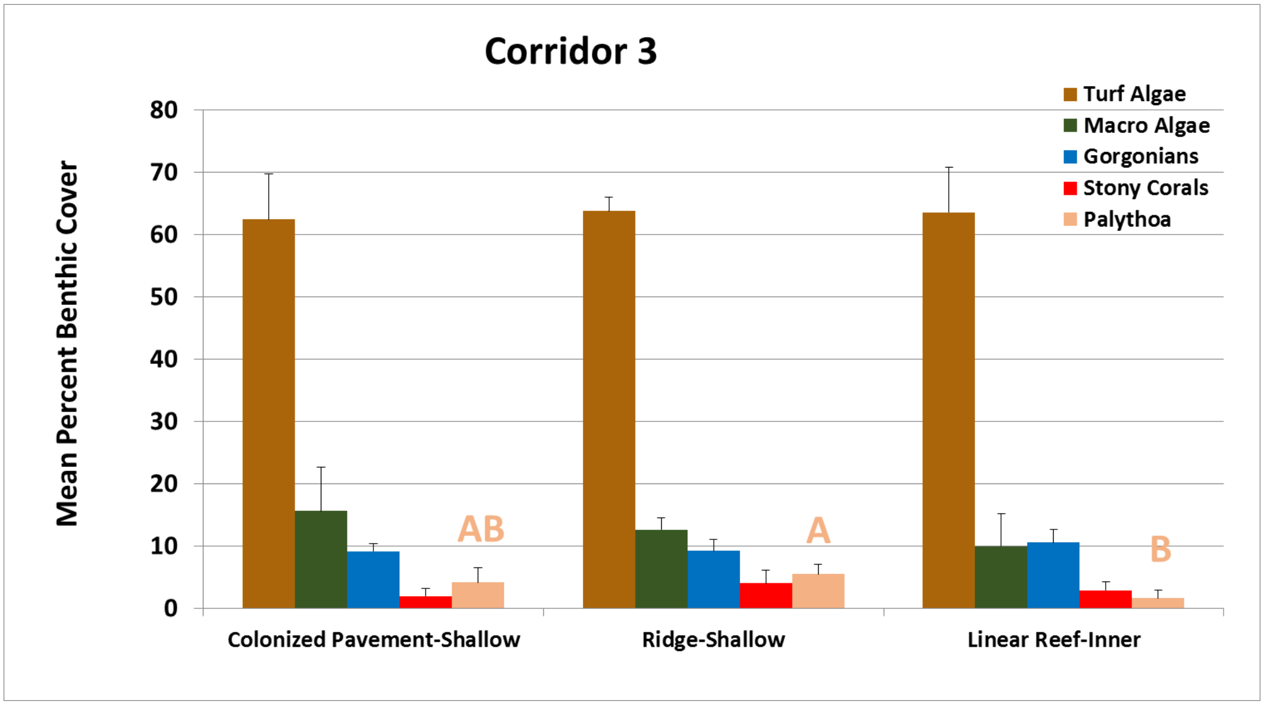
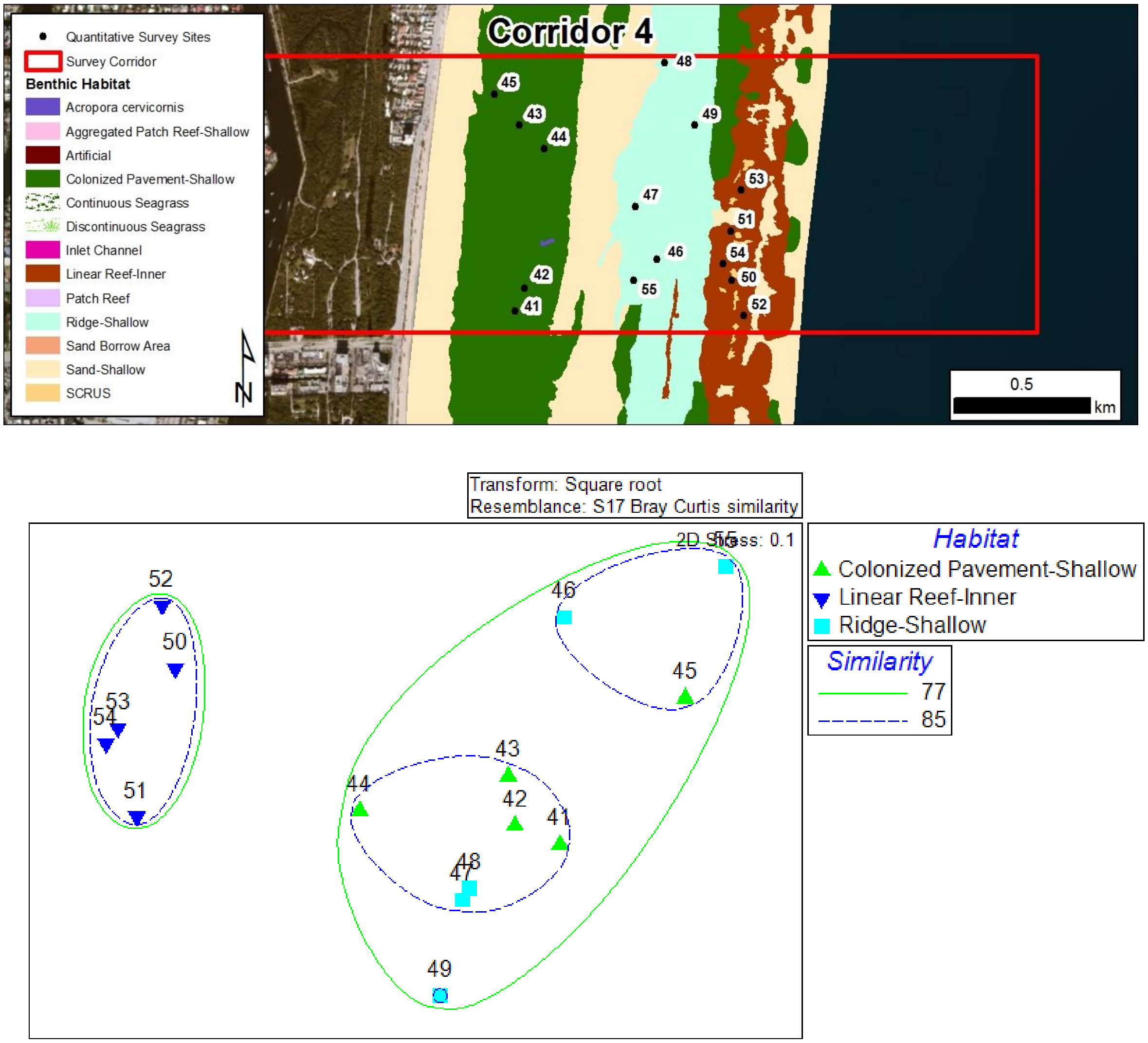


Figure 22. *Mean percent benthic cover for Corridor 3 by habitat. Error bars equal 1 standard deviation (σ). Letters denote significant differences between functional groups.*

4.3.9 Corridor 4 – Benthic Cover

In Corridor 4, Inner Reef sites were significantly different from the others (Figure 23). A similarity percentages (SIMPER) analysis (based off of square-root transformed data) indicated that the clustering of Inner Reef sites was driven by a high percentage of macroalgae ($\bar{x}$=33.30% ±3.06 SEM) versus Colonized Pavement ($\bar{x}$ = 10.90% ± 0.83 SEM) and Ridge ($\bar{x}$ = 9.45% ± 2.39 SM). Conversely, the Inner Reef had a lower percentage of turf algae ($\bar{x}$ = 39.25% ± 2.62 SEM) than was found on Colonized Pavement ($\bar{x}$ = 60.70% ± 2.69 SEM) and Ridge ($\bar{x}$ = 71.40% ± 2.39 SEM). The percent cover of *Palythoa* spp. also played a role in cover differences as the Inner Reef had the highest percentage ($\bar{x}$ = 12.85% ± 2.29 SEM), while both Colonized Pavement ($\bar{x}$ = 2.70% ± 1.29 SEM) and Ridge ($\bar{x}$ = 2.10% ± 0.94 SEM) had less. The MDS plot shows the Colonized Pavement sites to generally cluster together, while the Ridge sites are broken into a cluster of 3 and a cluster of 2. The MDS bubble plots show that these two Ridge sites did not have many gorgonians and stony corals, thus making them more like pavement (Figure 24).



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Habitat comparison		
Colonized Pavement-Shallow, Linear Reef-Inner	**0.932**	**0.8**
Colonized Pavement-Shallow, Ridge-Shallow	0.032	29.4
Linear Reef-Inner, Ridge-Shallow	**0.872**	**0.8**

Figure 23. *Corridor 4 multivariate analyses results. Top: map showing randomly stratified survey locations. Middle: MDS plot of the Bray-Curtis similarity matrix of percent benthic cover data. Bottom: tabular summary of analysis of similarity (ANOSIM) pairwise test between habitat types. Data treatment as in Figure 14.*

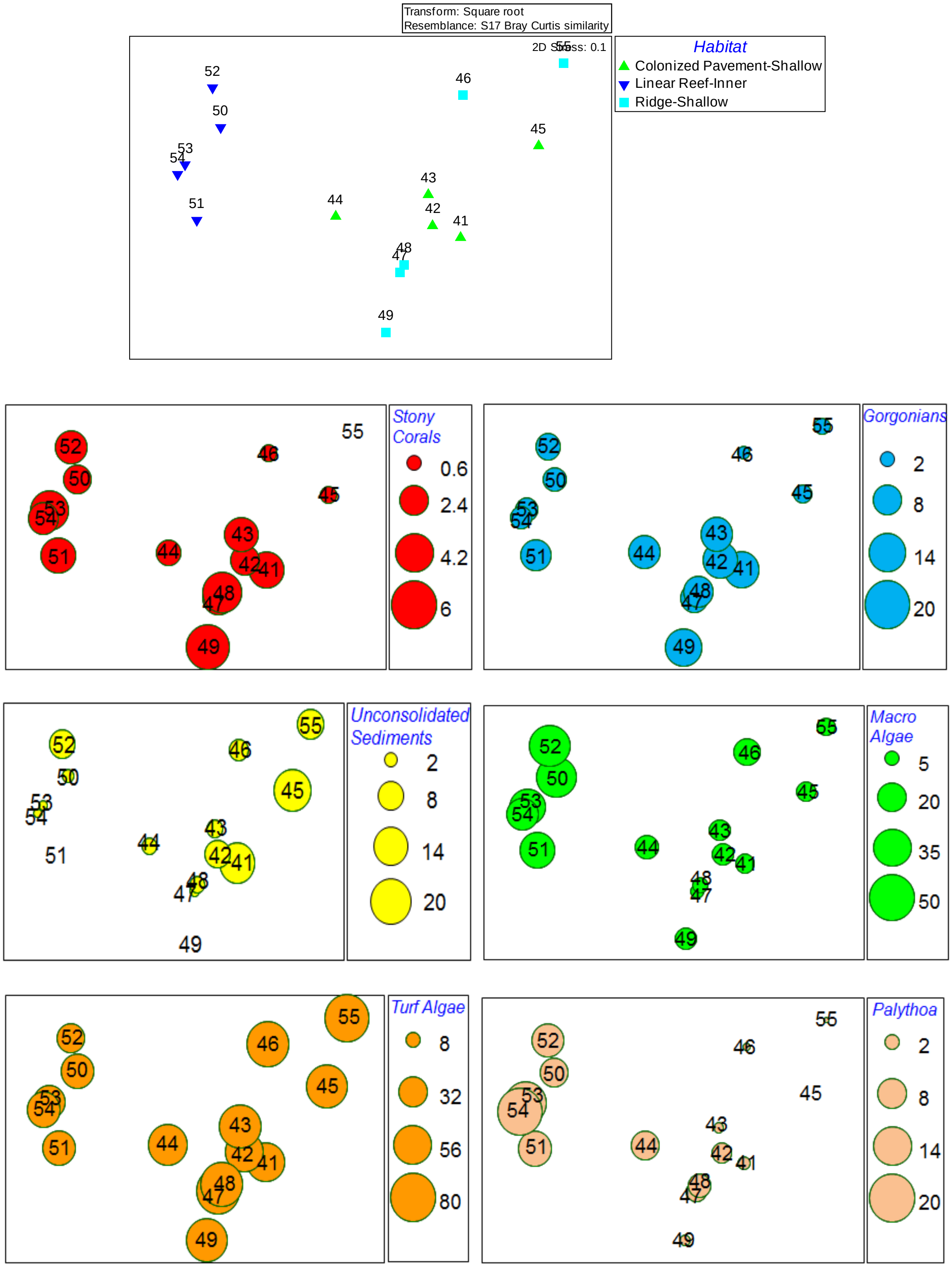


Figure 24. *Corridor 4 corresponding 2D bubble plots.*

Figure 25 represents mean percent benthic cover comparisons for Corridor 4 based on untransformed data. The Inner Reef habitat had significantly lower mean percent benthic cover values of turf algae (ANOVA, p = 0.0122) compared to all other habitats. The Inner Reef habitat also had significantly higher mean percent benthic cover values of macroalgae (ANOVA, p = 0.0122) and *Palythoa* spp. (ANOVA, p = 0.0160) compared to all other habitats.

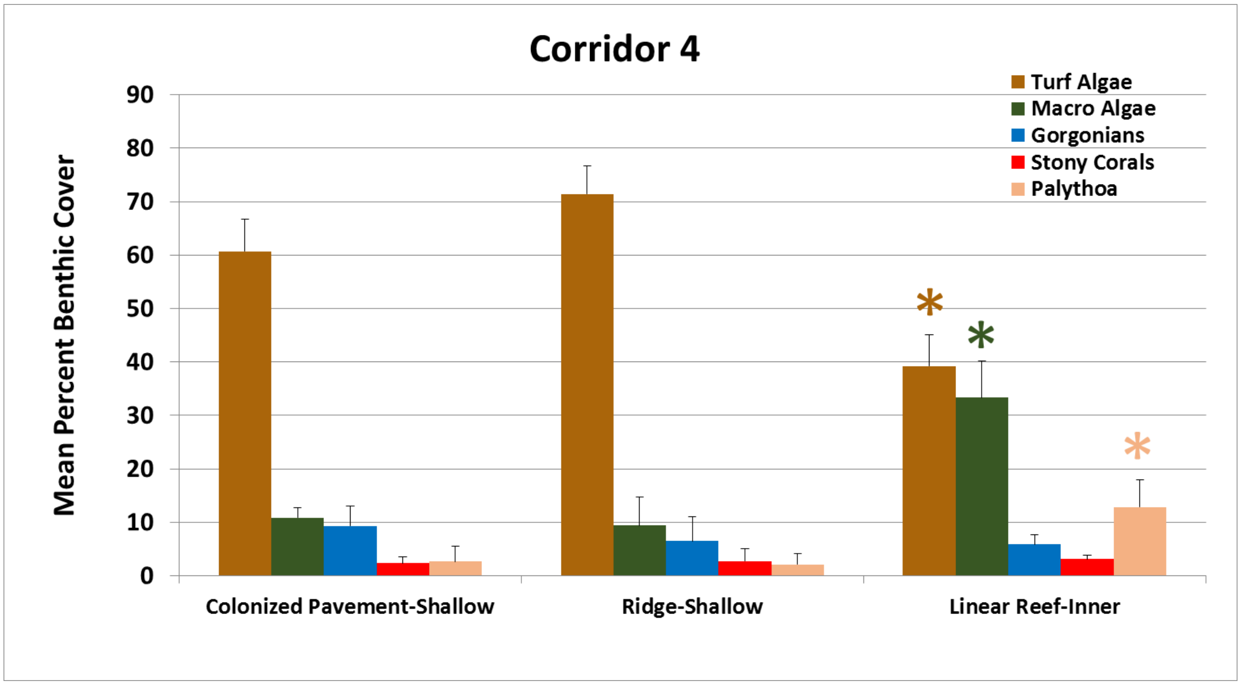
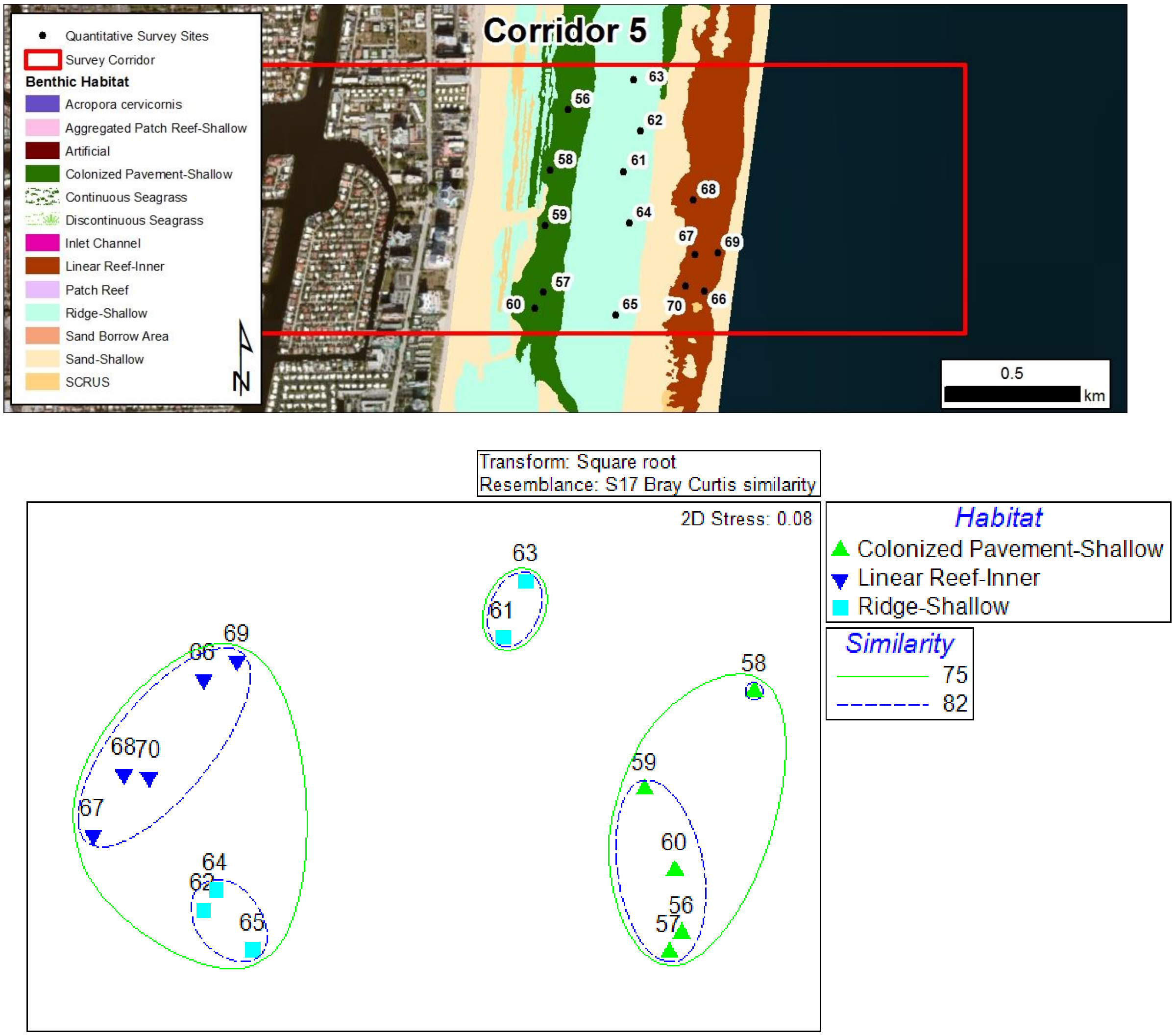


Figure 25. *Mean percent benthic cover for Corridor 4 by habitat. Error bars equal 1 standard deviation (σ). Asterisk denotes significant differences between functional groups.*

4.3.10 Corridor 5 – Benthic Cover

In Corridor 5, all habitat types exhibited significant clustering, grouping separately from each other (Figure 26). A similarity percentages (SIMPER) analysis (based off of square-root transformed data) indicated that the Inner Reef sites had a higher percentage of *Palythoa* spp. and gorgonians ($\bar{x}$ = 10.7% ± 3.85 SEM and $\bar{x}$ = 7.70% ± 1.35 SEM, respectively) than did the Colonized Pavement sites ($\bar{x}$ = 0.05% ± 0.05 SEM and $\bar{x}$ = 0.15% ± 0.06 SEM, respectively) and Ridge sites ($\bar{x}$ = 4.20% ± 2.23 SEM and $\bar{x}$ = 9.00% ± 3.07 SEM, respectively). The percent cover of turf algae decreased when moving off shore, with the Colonized Pavement sites having the highest ($\bar{x}$ = 85.30% ± 2.79 SEM), while the Ridge sites ($\bar{x}$ = 74.20% ± 7.93 SEM) and Inner Reef sites ($\bar{x}$ = 59.35% ± 2.05 SEM) had increasingly lower percentages. The MDS bubble plots show that the Inner Reef sites had the highest percentages of stony corals and sponges (Figure 27). The Ridge habitat had slightly lower values for these three substrates, while the Colonized Pavement had the lowest for these substrates. This explains why Ridge sites fell in between Inner Reef and Colonized Pavement sites.



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Habitat comparison		
Colonized Pavement-Shallow, Linear Reef-Inner	**1**	**0.8**
Colonized Pavement-Shallow, Ridge-Shallow	**0.82**	**0.8**
Linear Reef-Inner, Ridge-Shallow	**0.452**	**0.8**

Figure 26. *Corridor 5 multivariate analyses results. Top: map showing randomly stratified survey locations. Middle: MDS plot of the Bray-Curtis similarity matrix of percent benthic cover data. Bottom: tabular summary of analysis of similarity (ANOSIM) pairwise test between habitat types. Data treatment as in Figure 14.*

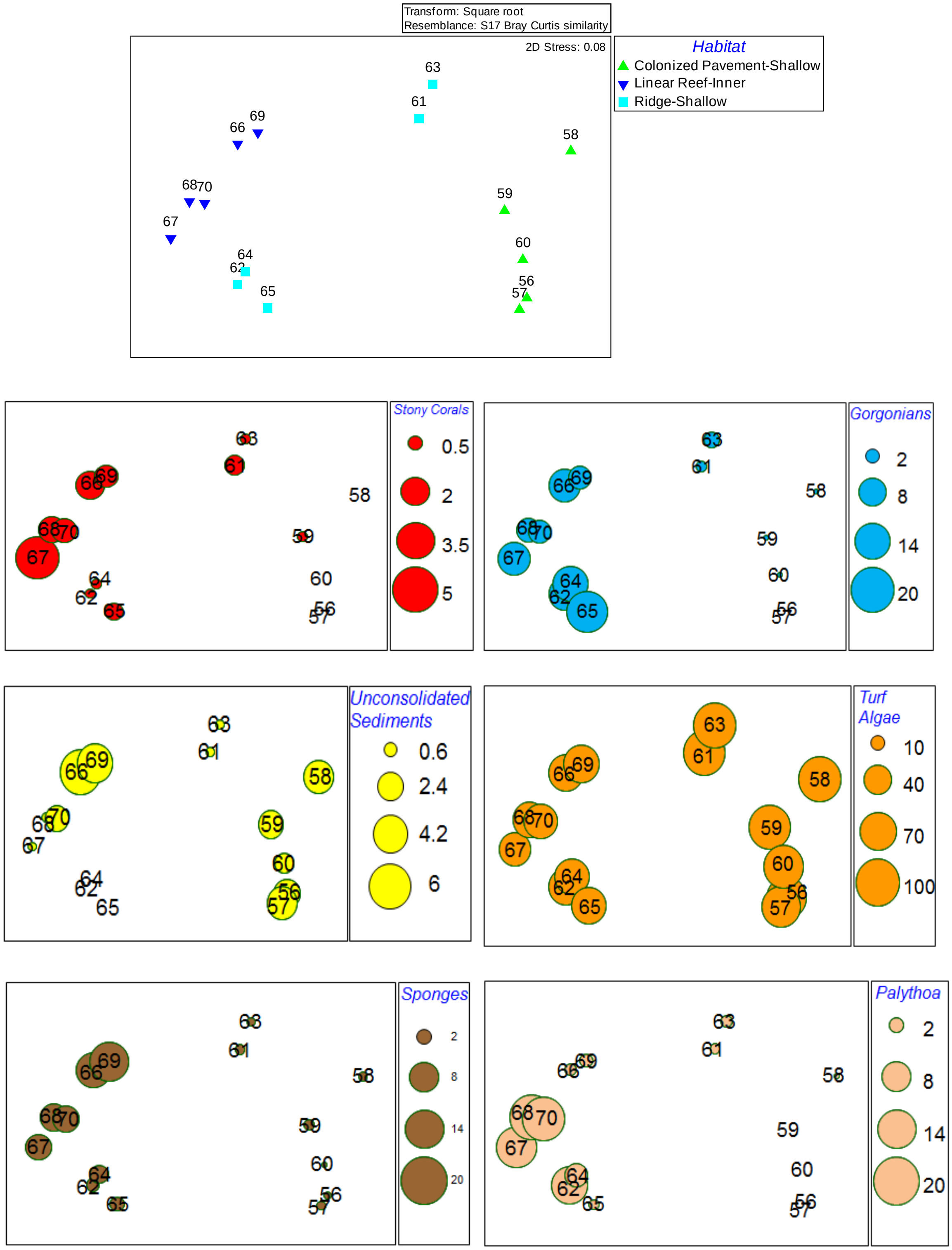


Figure 27. *Corridor 5 corresponding 2D bubble plots.*

Figure 28 represents mean percent benthic cover comparisons for Corridor 5 based on untransformed data. The Colonized Pavement habitat had significantly higher mean percent cover values of turf algae than the Inner Reef (ANOVA, p = 0.0122). The Colonized Pavement habitat also had significantly lower mean percent cover values of gorgonians (ANOVA, p = 0.0109) and *Palythoa* spp. (ANOVA, p = 0.0097) for both the Ridge and Inner Reef. All stony coral mean percent cover values were significantly different across all habitat types (ANOVA, p = 0.0193).

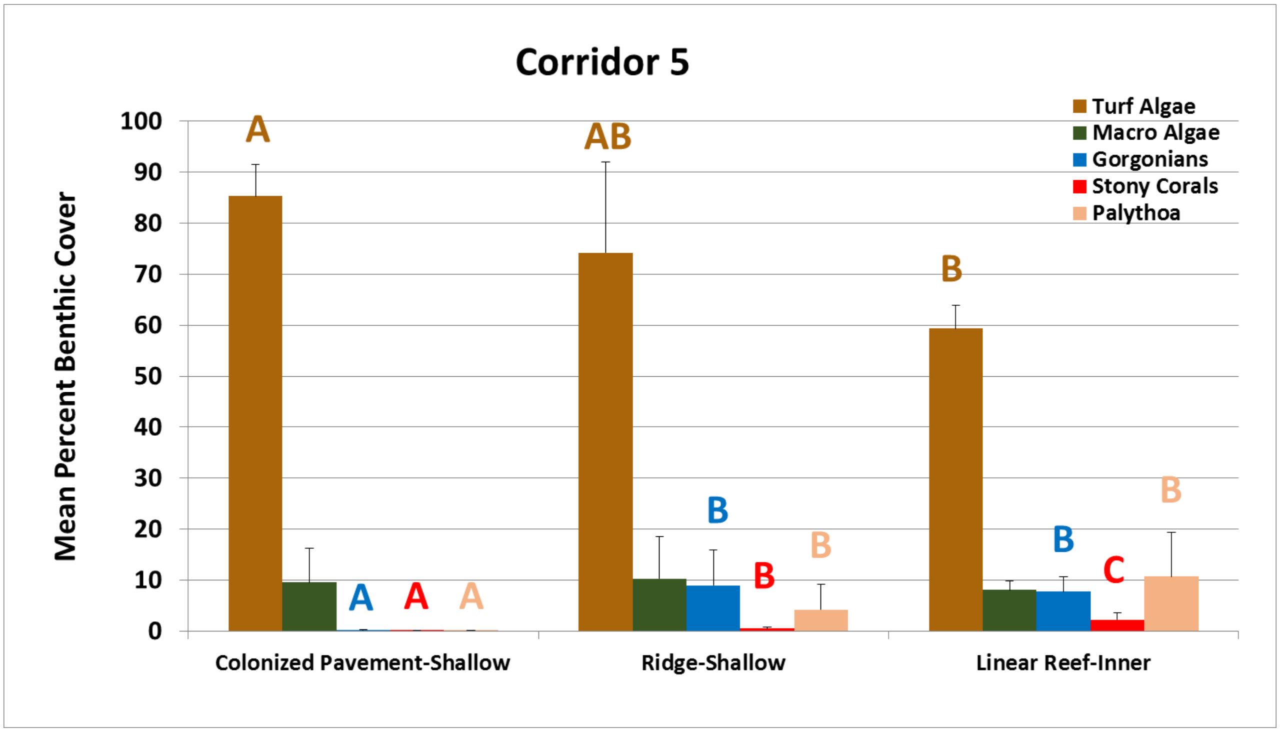


Figure 28. *Mean percent benthic cover for Corridor 5 by habitat. Error bars equal 1 standard deviation (σ). Letters denote significant differences between functional groups.*

4.4 Latitudinal Comparisons by Habitat

4.4.1 Stony Coral Mean Density

Corridor 1 had the highest mean coral density (x=1.73 ±0.27 SEM), although it was not significantly different from values for the other corridors (Corridor 2: x=0.89 ±0.22 SEM, Corridor 3: x=1.21 ±0.22 SEM, Corridor 4: x=1.28 ±0.22 SEM, Corridor 5: x=0.54 ±0.22 SEM). However, mean coral density varied by corridor within each habitat type (Figure 29). The Colonized Pavement mean coral density was lowest in Corridors 1 and 5 ($\bar{x}$ = 0.11 ± 0.17 SEM and $\bar{x}$ = 0.27 ± 0.17 SEM, respectively), and highest in Corridors 3 and 4 ($\bar{x}$ = 0.92 ± 0.17 SEM and $\bar{x}$ = 0.99 ± 0.17 SEM, respectively), with Corridor 1 significantly different from Corridors 3, 4 and 5 (ANOVA, p = 0.0122) and Corridor 5 significantly different from Corridors 3 and 4 (ANOVA, p = 0.0119). The Ridge mean coral density was highest in Corridors 3 and 4 ($\bar{x}$ = 1.56 ± 0.20 SEM and $\bar{x}$ = 0.77 ± 0.20 SEM, respectively), as on the Colonized Pavement, but lowest in Corridors 2 and 5 ($\bar{x}$ = 0.54 ± 0.20 SEM and $\bar{x}$ = 0.37 ± 0.20 SEM, respectively). Corridor 3 was significantly different than Corridors 2 and 5 (ANOVA, p = 0.0122). The Inner Reef differed in having the highest mean coral density in Corridor 1 ($\bar{x}$ = 3.34 ± 0.21 SEM), with lowest mean coral density in Corridor 5 ($\bar{x}$ = 0.99 ± 0.21 SEM), as on the Colonized Pavement and Ridge habitats. Corridor 1 was significantly different than all other Corridors (ANOVA, p = 0.0367). Corridor 3 was significantly different than Corridor 4 (ANOVA, p = 0.0216). Corridor 5 was significantly different than Corridor 2 and 4 (ANOVA, p = 0.0216).

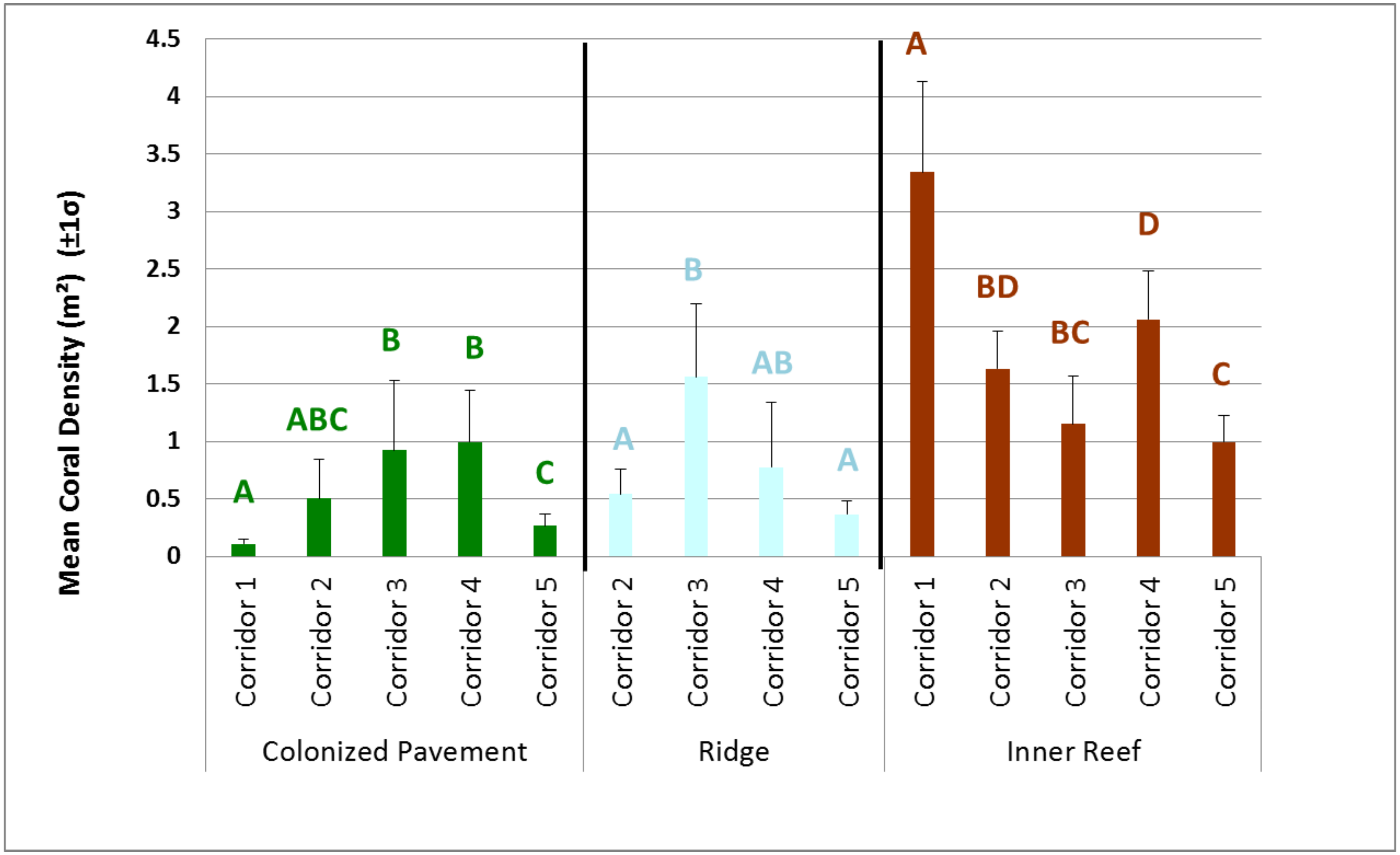


Figure 29. *Mean coral density by corridor and habitat. Corridors were organized from south (Corridor 1) to north (Corridor 5). Error bars equal 1 standard deviation (σ). Letters denote significant differences between corridors within habitats.*

4.4.2 Stony Coral Mean Species Richness

Mean coral species richness was similar in Corridors 1 - 4 (x̄ = 8.00 ± 0.99 SEM, x̄ = 8.07 ± 0.81 SEM, x̄ = 8.87 ± 0.81 SEM, and x̄ = 8.27 ± 0.81 SEM, respectively) and lower in Corridor 5 (x̄ = 6.07 ± 0.81 SEM). However, Corridor 5 mean species richness was only significantly lower than in Corridor 3 (ANOVA, p = 0.0186). Mean richness also varied within each habitat by corridor (Figure 30). On the Colonized Pavement, Corridors 3 and 4 had the highest mean richness (x̄ = 7.40 ± 0.76 SEM and x̄ = 6.40 ± 0.76 SEM, respectively), while Corridors 1 and 5 had the lowest (x̄ = 3.8 ± 0.76 SEM and x̄ = 2.20 ± 0.76 SEM, respectively), with the Corridor 5 value signficantly different than Corridors 2-4 (ANOVA, p = 0.0129) and Corridor 1 significantly different than Corridor 3 (ANOVA, p = 0.0459). The Ridge habitat was similar in having the highest mean richness in Corridor 3 (x̄ = 9.60 ± 0.42 SEM) and the lowest in Corridor 5 (x̄ = 5.6 ± 0.42 SEM). Mean richness in the Corridor 5 Ridge habitat was significantly lower than in all the other Corridors in this habitat (ANOVA, p = 0.0227), and Corridor 3 was significantly different than Corridor 4 (ANOVA, p = 0.0181). The only significant difference among Inner Reef sites was higher richness on Corridor 1 (x̄ = 12.20 ± 0.67 SEM) than on Corridor 3 (x̄ = 9.60 ± 0.67 SEM) (ANOVA, p = 0.0141).

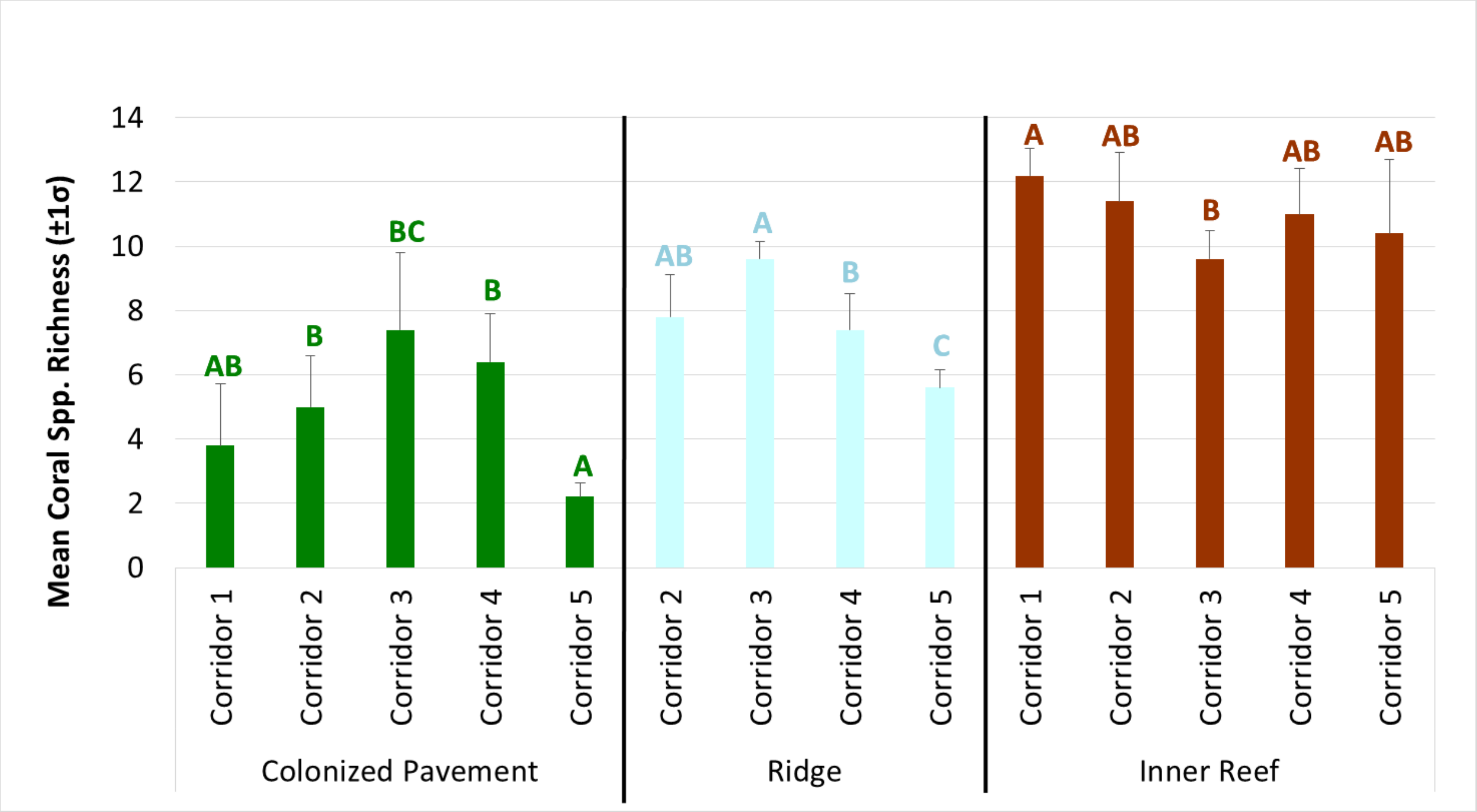


Figure 30. *Mean number of coral species by corridor and habitat. Corridors, error bars and letters as in Figure 29.*

4.4.3 Stony Coral Mean Density of Most Abundant Species

This study recorded 22 stony coral species, with *Porites astreoides* (29.7%), *Siderastrea siderea* (17.5%), and *Acropora cervicornis* (10.3%) together accounting for the majority of colonies measured (57.5%) (Table 2).

Porites astreoides mirrored the pattern discussed above for mean coral density (Figure 31), with both the Colonized Pavement and Ridge having higher densities in Corridors 3 and 4, while the Inner Reef had the highest density in Corridor 1. As the most abundant species, *P. astreoides* may have driven the overall coral density trend. Its density was significantly higher on the Inner Reef than on either the Ridge and Colonized Pavement (ANOVA, $p = 0.0154$) and was lowest on the Colonized Pavement ($\bar{x} = 0.21 \pm 0.14$ SEM), intermediate on the Ridge ($\bar{x} = 0.32 \pm 0.11$ SEM), and greatest on the Inner Reef ($\bar{x} = 0.62 \pm 0.09$ SEM). .

Siderastrea siderea also contributed to the total mean density trend on Corridor 1, with the highest mean density on the Inner Reef (Figure 31). Mean density of *S. siderea* was significantly different in all habitat types (ANOVA, $p = 0.0276$): lowest on the Colonized Pavement ($\bar{x} = 0.08 \pm 0.02$ SEM), followed by the Ridge ($\bar{x} = 0.12 \pm 0.03$ SEM), and was greatest on the Inner Reef ($\bar{x} = 0.37 \pm 0.02$ SEM).

Although it was one of the most abundant/dense species, *A. cervicornis* was only found in Corridors 2, 3, and 4 (Figure 31). Mean *A. cervicornis* density was highest on the Colonized Pavement ($\bar{x} = 0.45 \pm 0.10$ SEM), followed by the Ridge ($\bar{x} = 0.29 \pm 0.09$ SEM), and was lowest the Inner Reef ($\bar{x} = 0.14 \pm 0.18$ SEM). Of the 471 colonies counted, only 25 (5.3%) occurred on Inner Reef sites, 235 (49.9%) on Colonized Pavement and 211 (44.8%) on Ridge sites.

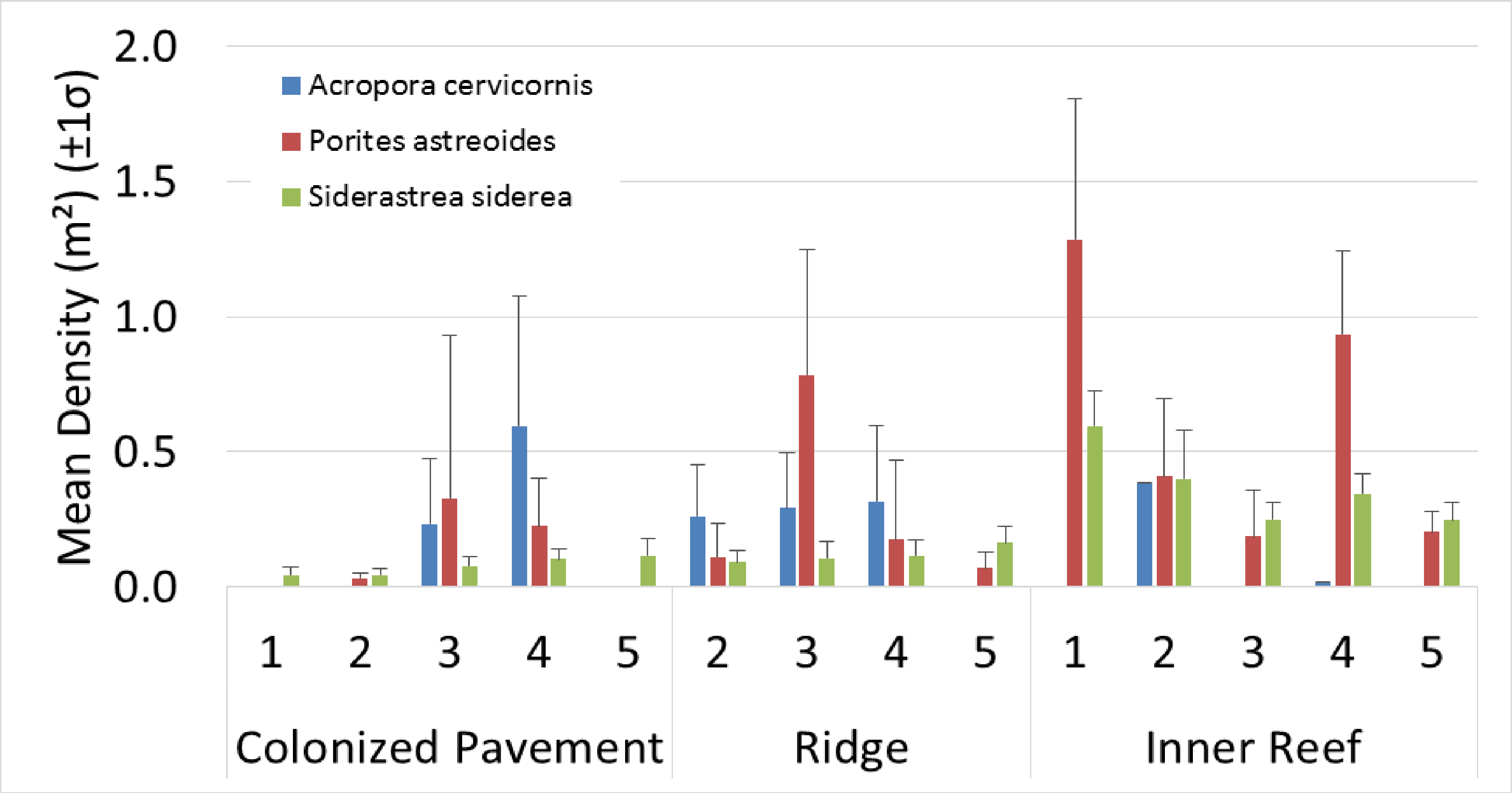


Figure 31. *Mean density of the three most abundant stony coral species by corridor and habitat. Corridors and error bars as in Figure 29.*

4.4.4 Gorgonian Mean Density

Gorgonian densities varied within habitat types and among corridors, with fans least common throughout and rods outnumbering plumes except on the Inner Reef on Corridor 1(Figure 32). On the Colonized Pavement, fans were densest in Corridors 3 and 4 and were absent in Corridor 1. Plumes were denser in the three southern Corridors and rare in Corridor 5. Rod densities were greatest in Corridors 2 and 3 and, like plumes, they were rare in Corridor 5. On the Ridge habitat, fans were present in all Corridors. Plumes again had a higher density in the southern Corridors, while rod densities were greatest in Corridors 2 and 5. On the Inner Reef, fans were densest in Corridors 4 and 5, plumes densest in Corridor 1, and rods similarly dense in Corridors 1, 3, 4 and 5.

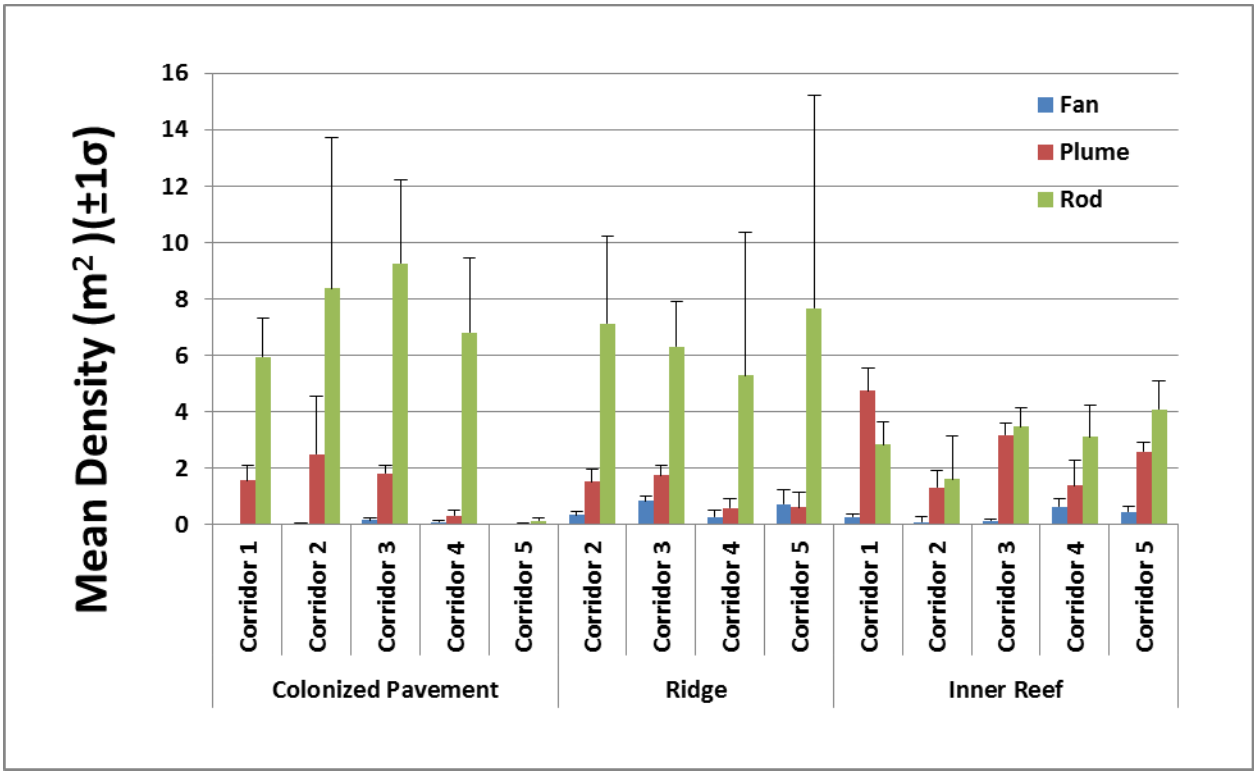


Figure 32. *Mean gorgonian density by type, corridor and habitat. Corridors and error bars as in Figure 29.*

In the Colonized Pavement habitat (Figure 33), fan densities were significantly lower in Corridors 1, 2, and 5 than in Corridors 3 and 4 (ANOVA, p = 0.0075; p = 0.0439; and p = 0.0109 resepctively). Plumes were significantly less dense in Corridor 4 and 5 than in the others (ANOVA, p = 0.0122 and p = 0.0117). Rods in Corridor 5 were significantly less dense than in the others (ANOVA, p = 0.0119).

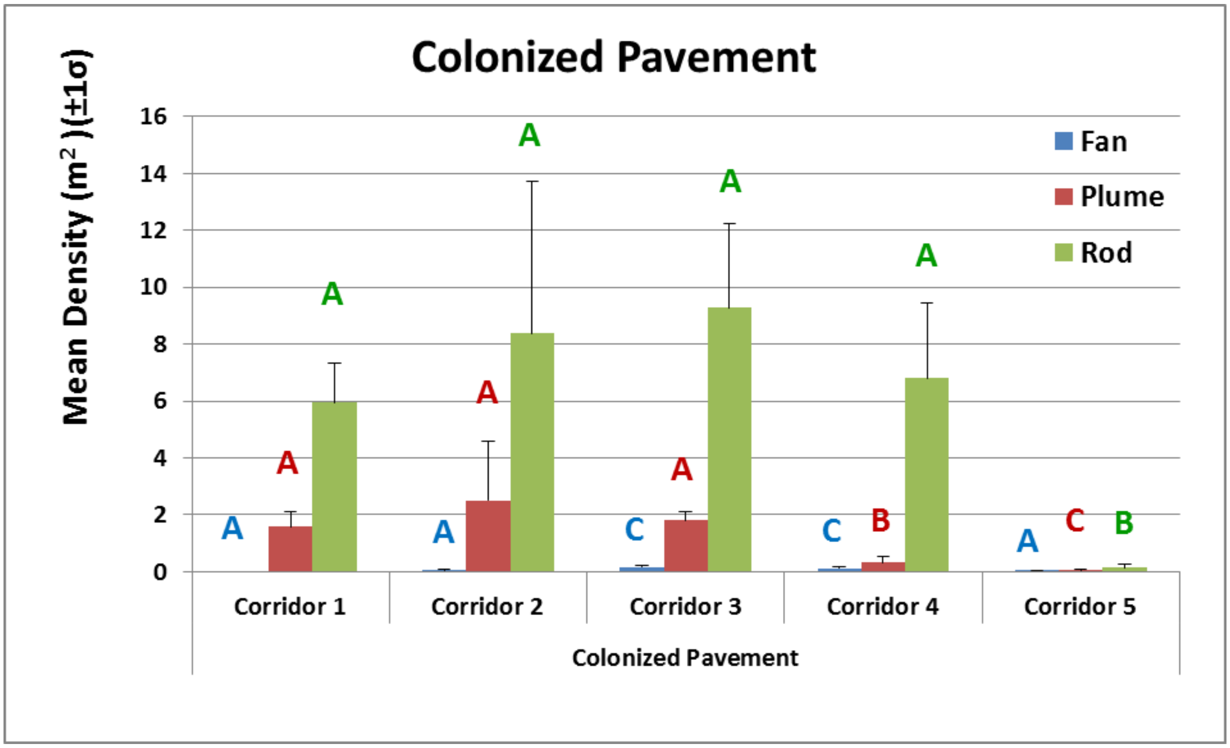


Figure 33. *Mean gorgonian density for Colonized Pavement by corridor and morphotype. Corridors, error bars and letters as in Figure 29.*

In the Ridge habitat (Figure 34) fan density in Corridor 3 was significantly greater than in Corridors 2 and 4 (ANOVA, p = 0.0119). Plumes in Corridors 4 and 5 were significantly less dense than Corridors 2 and 3 (ANOVA, p = 0.0122 and p = 0.0160). No significant differences were found in rods between Corridors.

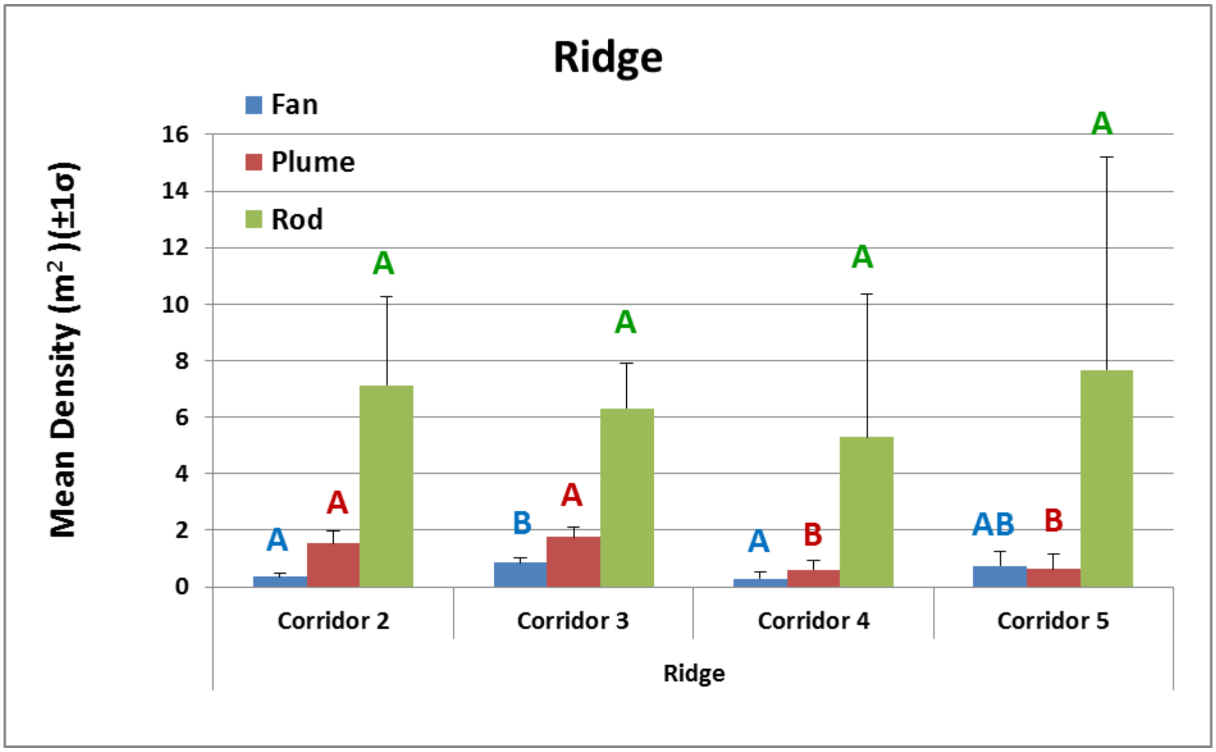


Figure 34. *Mean gorgonian density for the Ridge by Corridor and morphotype. Corridors, error bars and letters as in Figure 29.*

On the Inner Reef (Figure 35), fans were significantly less dense in Corridors 1, 2 and 3 than Corridor 4 (ANOVA, p = 0.0465). In Corridors 2 and 3, fans were significantly less dense than Corridor 4 and 5 (ANOVA, p = 0.0361). Plumes were significantly denser in Corridor 1 than in all other Corridors (ANOVA, p = 0.0157). In Corridor 3, plume density was significantly higher than in Corridors 2, 4 and 5 (ANOVA, p = 0.0361). In Corridor 5, plumes were significantly denser than in Corridors 2 and 4 (ANOVA, p = 0.0216). Rods exhibited no significant density differences among Corridors.

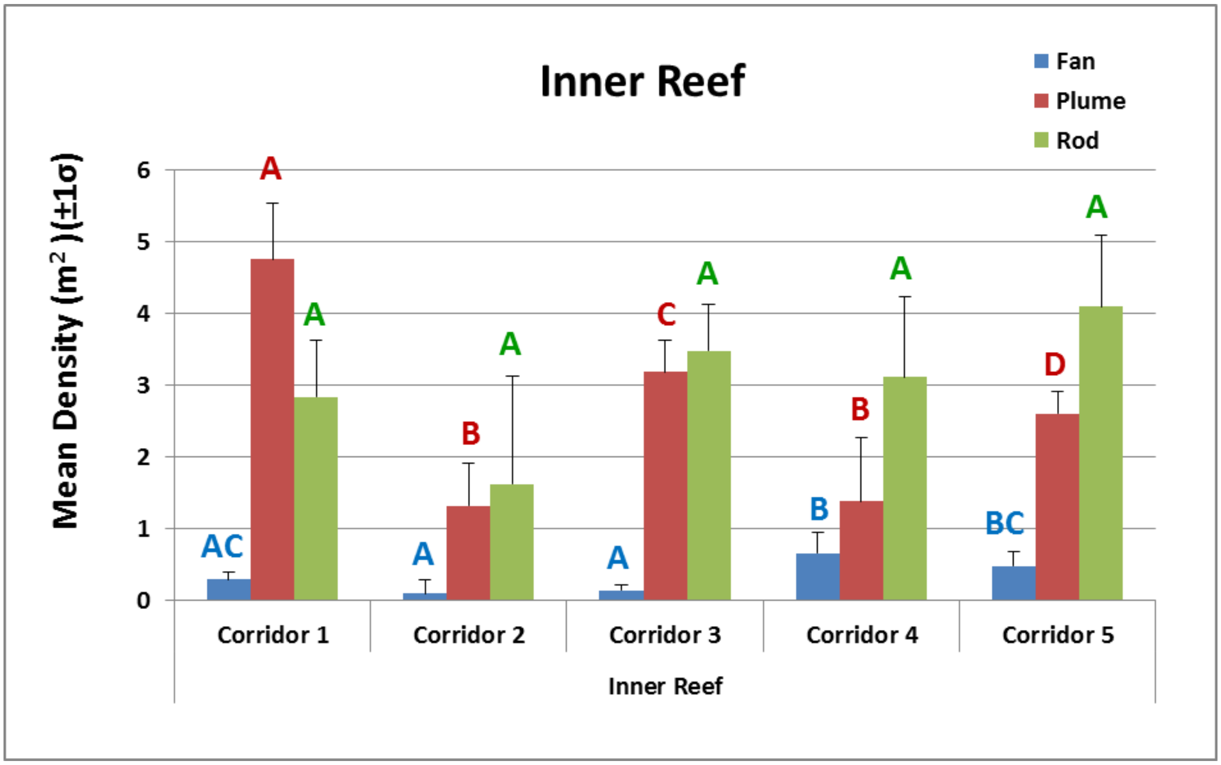


Figure 35. *Mean gorgonian density for the Inner Reef by Corridor and morphotype. Corridors, error bars and letters as in Figure 29.*

4.4.5 Gorgonian Mean Density by Size Class and Morphotype

Fan gorgonians had the lowest mean densities in Corridor 1 for the 4-10-cm and 11-25-cm height classes (Figure 36). Fans 4-10 cm and 26-50 cm in height were densest in Corridor 5, while fans 11-25 cm and >50 cm in height were densest in Corridor 3. Plume mean density was greatest in Corridor 3 for the 4-10-cm and 11-25-cm classes, suggesting a possibly younger population of species with this form (likely chiefly *Antillogorgia* sp.) here relative to other Corridors. Plumes in Corridor 4 had the lowest mean density for the 4-10-cm, 11-25-cm, and >50-cm classes. It is noteworthy that the taller plumes (26-50-cm and >50-cm classes) in Corridor 1 had higher mean densities than rods. In all other cases, rods had higher mean densities than both fans and plumes, in all 4 size classes and in all Corridors. In Corridor 1, smaller rods (4-10-cm and 11-25-cm classes) had the lowest mean densities, perhaps because extremely dense plume populations here reduced the success of rod recruitment or competition. Rods were found in highest densities in Corridor 1 for the 26-50 cm and >50 cm size bins. Significant differences among gorgonian densities by height class are summarized below.

4 – 10 cm: Fan density in both Corridors 1 and 2 were significantly lower than Corridors 3, 4, and 5 (ANOVA, $p = 0.0374$ and ANOVA, $p = 0.0163$, respectively), however they were not significantly different from each other. Plumes in Corridors 2, 3 and 4 were all significantly different from each other (ANOVA, $p = 0.0159$, ANOVA, $p = 0.0113$ and ANOVA, $p = 0.0159$, respectively) but similar to the remaining Corridors. Rods in Corridor 1 were significantly lower than Corridors 2, 3, and 4 (ANOVA, $p = 0.0350$). Corrdor 3 was also significantly higher than Corridors 2 and 5 (ANOVA, $p = 0.0442$).

11 – 25 cm: Fan density in Corridor 2 were significantly different than Corridors 3 and 4 (ANOVA, $p = 0.0494$). Plumes in Corridor 4 were significantly lower than Corridors 1, 2, and 3 (ANOVA, $p = 0.0065$). Corridor 5 was also significantly lower than Corridors 1 and 3 (ANOVA, $p = 0.0246$). Rods in Corridor 3 were significantly higher than Corridor 5 (ANOVA, $p = 0.0264$).

26 – 50 cm: No significant differences in fan density was found between Corridors. Plumes in Corridors 1, 2, and 3 were all significantly higher than Corridors 4 and 5 (ANOVA, p = 0.0190), and also significantly different from each other (ANOVA, p = 0.0360). Rods in Corridor 5 were significantly different than Corridors 1 and 3 (ANOVA, p = 0.0463).

>50 cm: No significant differences in fan density was found between Corridors. Plumes in Corridor 1 were significantly higher than all other Corridors (ANOVA, p = 0.0184). Corridor 4 was also significantly lower than Corridors 2 and 3 (ANOVA, p = 0.0314). Rods in Corridor 5 were significantly lower than Corridors 1, 2, and 3 (ANOVA, p = 0.0412). Corridor 4 was also significantly lower than Corridors 1 and 3 (ANOVA, p = 0.0360).

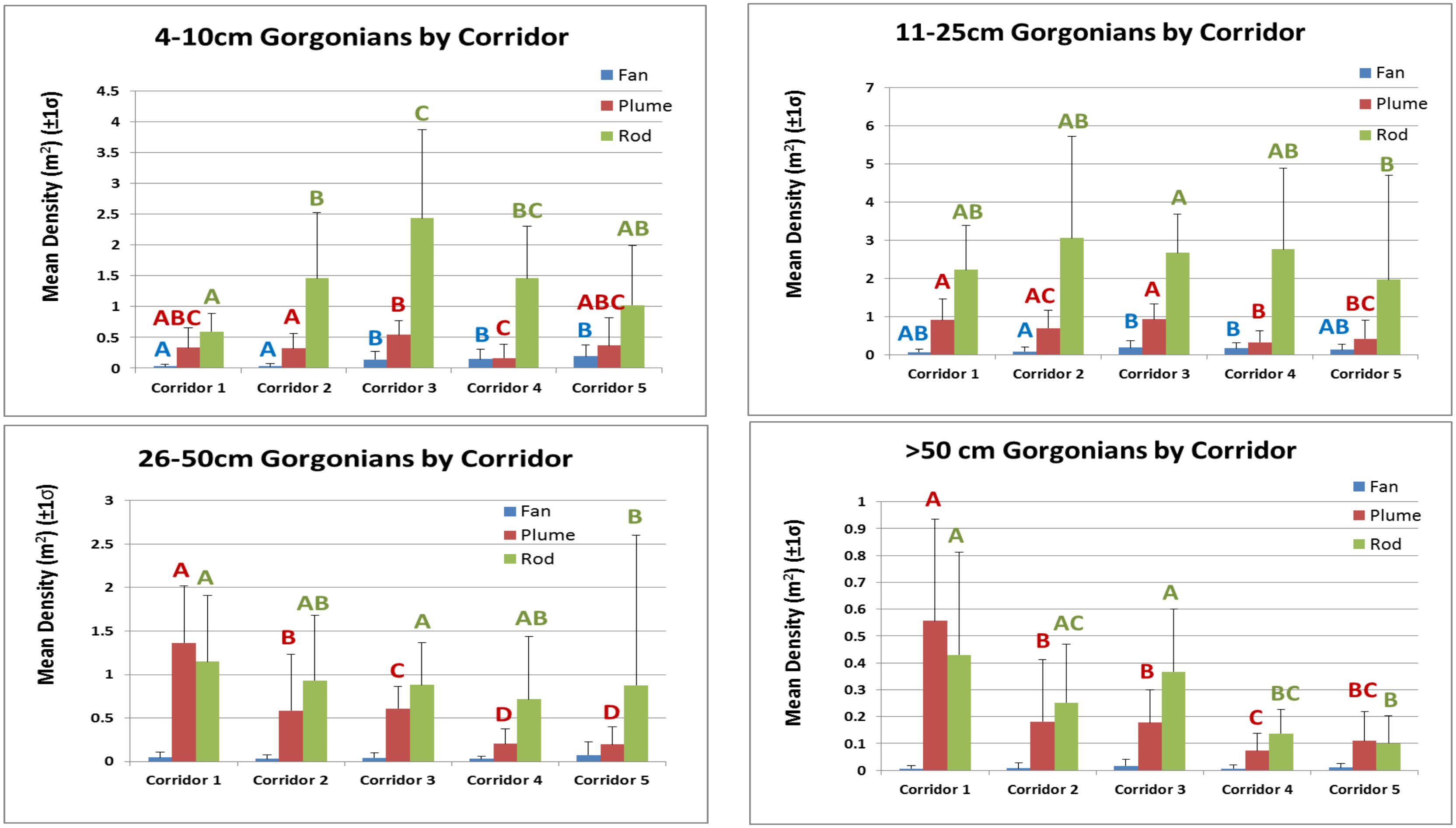


Figure 36. *Graphs for each size class illustrating mean gorgonian density by corridor and morphotype. Corridors, error bars and letters as in Figure 29.*

4.4.6 Mean Sponge Density

Mean densities of *X. muta* varied among Corridors and by habitats within Corridors (Figure 37). In the Colonized Pavement, *X. muta* was only found in Corridor 4 ($\bar{x} = 0.02 \pm 0.004$ SEM). In the Ridge habitat, *X. muta* was recorded in Corridors 2, 3, and 4, with Corridor 4 having the highest density ($\bar{x} = 0.07 \pm 0.015$ SEM), and with significant differences in mean density only between the higher value in Corridor 4 relative to Corridor 5 (ANOVA, $p = 0.0254$). Mean densities of *X. muta* were greatest on the Inner Reef, with Corridor 2 having the highest density compared to the other Corridors ($\bar{x} = 0.23 \pm 0.05$ SEM). On the Inner Reef, mean density was significantly lower on Corridor 1 than in all other Corridors (ANOVA, $p = 0.0432$).

Cliona spp. mean density also varied by Corridor and habitat (Figure 37). In the Colonized Pavement habitat, *Cliona spp*. was solely found in Corridors 2, 3, and 4, with Corridor 3 having the highest mean density ($\bar{x} = 0.08 \pm 0.02$ SEM) but there were no significant differences among corridors. On the Ridge habitat it was again found only in Corridors 2, 3, and 4 but with highest mean density on Corridor 2 ($\bar{x} = 0.03 \pm 0.01$ SEM) and with significant differences only between the higher density on Corridor 2 relative to Corridor 5 (ANOVA, $p = 0.0248$). On the Inner Reef habitat, Corridor 1 had the highest density ($\bar{x} = 0.09 \pm 0.02$ SEM), which was significantly greater than that of Corridor 5 ($\bar{x} = 0.02 \pm 0.02$ SEM) (ANOVA, $p = 0.0112$).

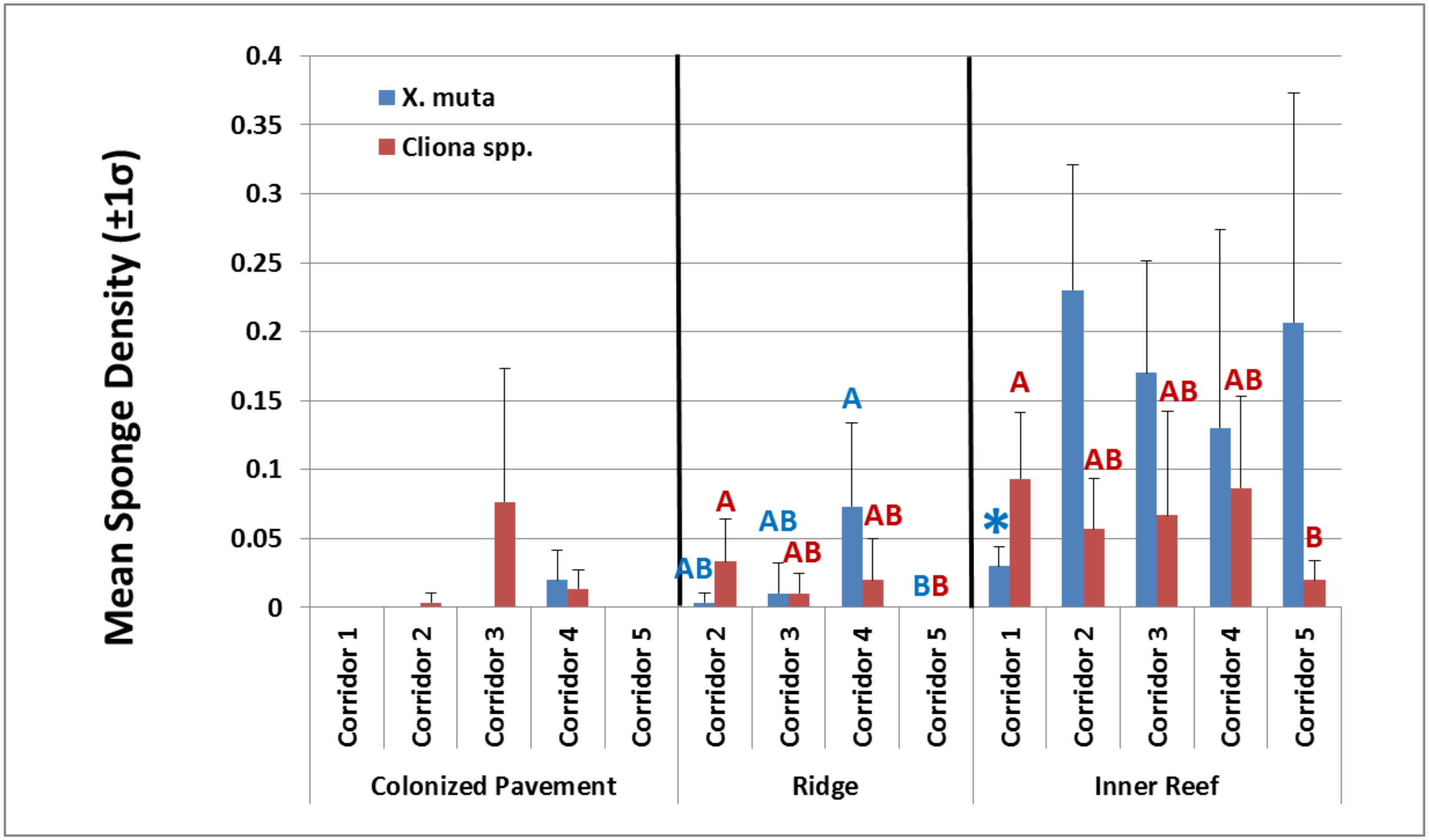
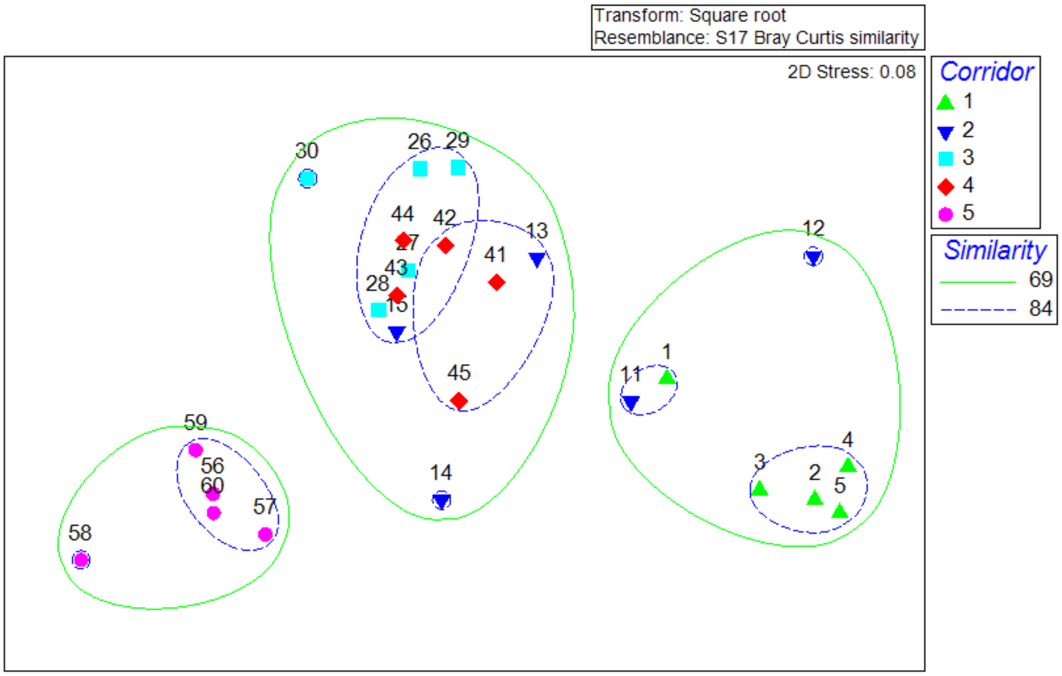


Figure 37. *Mean sponge density by corridor and habitat. Corridors, error bars and letters as in Figure 29.*

4.4.7 Colonized Pavement – Benthic Cover

Comparisons of benthic cover percentages between all sites in a given habitat type were conducted to evaluate latitudinal community differences. For Colonized Pavement sites, all Corridors differed significantly from one another except Corridors 2 and 4, which clustered together in the MDS plot (Figure 38), indicating that within- and between-Corridor variability were similar. A similarity percentages (SIMPER) analysis (based on square-root transformed data) indicated that Corridor 1 differed significantly from the others due to the presence of seagrass, which was found in Corridor 1 Colonized Pavement sites only. This is boldly illustrated in the MDS plot, as almost all of these sites are tightly grouped together. Corridor 5 sites also clustered tightly and differed distinctly from all other Corridors due to their having the highest turf algae percentage, the lowest gorgonian and sponge percentages, and no stony corals or *Palythoa* spp. Corridor 3 differed significantly from all other Corridors due to having the lowest percentage of unconsolidated sediments, as well as the highest percentage of *Palythoa* spp ($\bar{x}$ = 4.15% ± 1.05 SEM). *Palythoa spp.* was also present in Corridor 4 ($\bar{x}$ = 2.70% ± 1.29 SEM) but was absent from Corridors 1, 2 and 5. Percentage cover of turf algae increased with increasing latitude (Corridor 1: $\bar{x}$ = 23.25% ± 3.29 SEM, Corridor 2: $\bar{x}$ = 46.90% ± 11.08 SEM, Corridor 3: $\bar{x}$ = 62.40% ± 3.30 SEM, Corridor 4: $\bar{x}$ = 60.70% ± 2.69 SEM, Corridor 5: $\bar{x}$ = 85.30% ± 2.79 SEM), whereas the percent cover of macroalgae decreased with increasing latitude (Corridor 1: $\bar{x}$ = 35.45% ± 1.93 SEM, Corridor 2: $\bar{x}$ = 16.95% ± 5.94 SEM, Corridor 3: $\bar{x}$ = 15.60% ± 3.17 SEM, Corridor 4: $\bar{x}$ = 10.90% ± 0.83 SEM, Corridor 5: $\bar{x}$ = 9.55% ± 3.02 SEM). Clustering of Corridors 2 and 4 sites in the MDS bubble plot reflects their similar abundances of gorgonians, turf algae, and macroalgae (Figure 39).



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Corridor comparison		
1, 2	**0.684**	**0.8**
1, 3	**1**	**0.8**
1, 4	**1**	**0.8**
1, 5	**1**	**0.8**
2, 3	**0.44**	**0.8**
2, 4	0.136	12.7
2, 5	**0.88**	**0.8**
3, 4	**0.288**	**4.8**
3, 5	**1**	**0.8**
4, 5	**1**	**0.8**

Figure 38. *Colonized Pavement multivariate analyses results. Top: MDS plot of the Bray-Curtis similarity matrix of the percent benthic cover data of all colonized pavement sites. Outlines represent 69% and 84% similarity from the cluster analysis. Bottom: table summarizes the analysis of similarity (ANOSIM) pairwise test between corridors. Treatments as in Figure 15.*

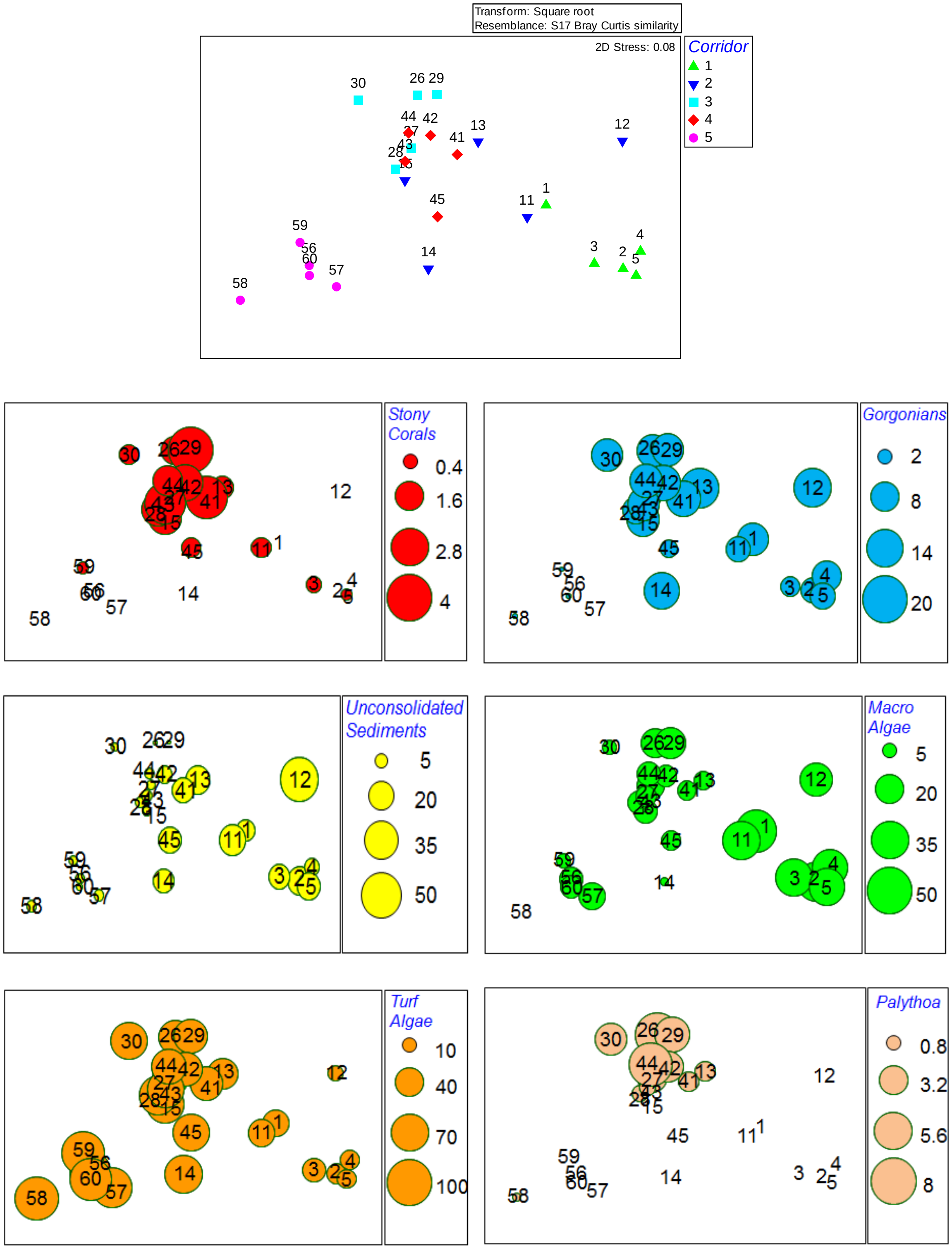


Figure 39. *Colonized Pavement corresponding 2D bubble plots.*

Figure 40 compares mean percent benthic cover of the different functional groups on Colonized Pavement in the different Corridors based on untransformed data. Mean percent cover by turf algae was significantly greater in Corridor 5 than in all other habitats (ANOVA, p = 0.0122) but was significantly lower in Corridor 1 than in Corridors 3 and 4 (ANOVA, p = 0.0122). By contrast, macroalgal cover was significantly greater in Corridor 1 than in Corridors 3, 4, and 5 (ANOVA, p = 0.0122). Gorgonians contributed significantly less cover to Corridor 5 than in all other Corridors (ANOVA, p = 0.0107). Seagrass was present only in Corridor 1 and its cover was significantly greater than in all other Corridors (ANOVA, p = 0.0075). Unconsolidated sediment cover was significantly greater in Corridor 1 than in Corridors 3 and 5 (ANOVA, p = 0.0119) and also in Corridor 4 compared to Corridor 3 (ANOVA, p = 0.0273).

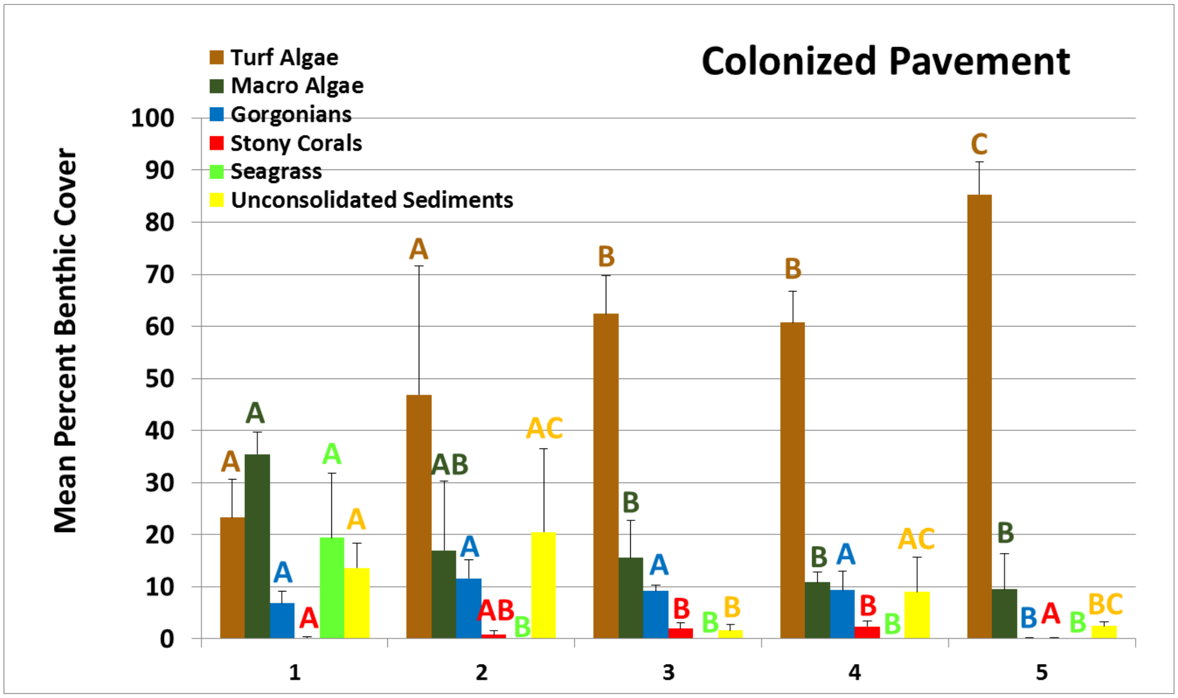
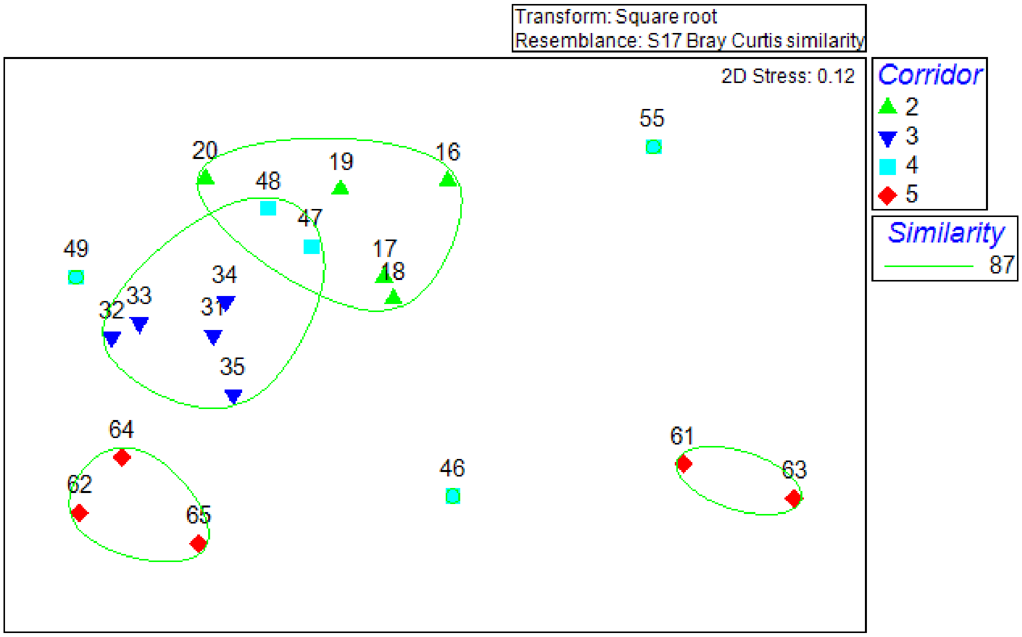


Figure 40. *Mean percent benthic cover for Colonized Pavement by corridor. Corridors, error bars and letters as in Figure 29.*

4.4.8 Ridge – Benthic Cover

In the MDS plot, Ridge sites in Corridors 2 and 3 clustered together (Figure 41); Corridor 4 sites were spread out, indicating a high level of between-site variability; and Corridor 5 sites appeared as two widely separated clusters. In the SIMPER analysis (based on square-root transformed data), despite clustering with Corridor 3, Corridor 2 differed significantly from all the others, except highly variable Corridor 4, chiefly from its having the lowest percent cover of macroalgae and *Palythoa spp*. and highest cover of sponges and gorgonians. Corridor 4's variability can be attributed to intermediate values for gorgonians, macro algae and *Palythoa* spp. and high percentage cover of sponges. Corridor 3 also differed significantly from all the others, reflecting its highest percent cover of macroalgae, stony corals, and *Palythoa spp.,* and lowest cover of turf algae. Corridor 5 differed significantly from all the others, excluding Corridor 4, due to its having the highest percent cover of turf algae and lowest stony coral cover. Its two distinct clusters within the MDS plot are a function of the higher cover of macroalgae and gorgonians at sites 62, 64,and 65, and higher cover of unconsolidated sediment at sites 61 and 63 (Figure 42).



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Corridor comparison		
2, 3	**0.896**	**0.8**
2, 4	0.168	11.9
2, 5	**0.436**	**0.8**
3, 4	**0.308**	**1.6**
3, 5	**0.452**	**0.8**
4, 5	0.18	13.5

Figure 41. *Ridge multivariate analyses results. Top: MDS plot of the Bray-Curtis similarity matrix of the percent benthic cover data of all colonized pavement sites. Outlines represent 87% similarity from the cluster analysis. Bottom: table summarizes the analysis of similarity (ANOSIM) pairwise test between corridors. Treatments as in Figure 15.*

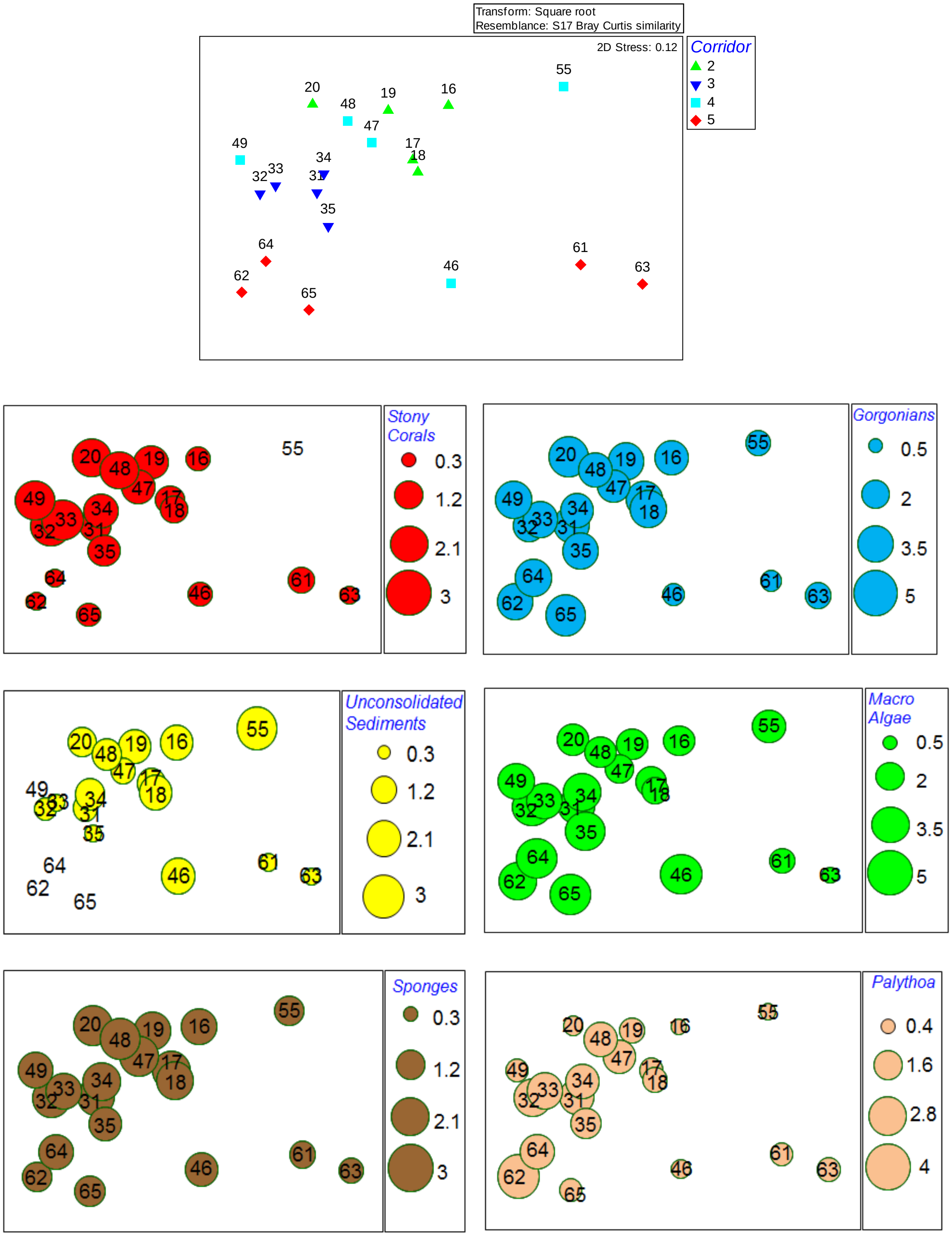


Figure 42. *Ridge corresponding 2D bubble plots.*

Figure 43 represents mean percent benthic cover comparisons for the Ridge habitat based on untransformed data. Corridor 4 had significantly higher mean percent benthic cover values for turf algae compared to Corridor 3 (ANOVA, p = 0.0216). Corridor 3 had significantly higher values for macroalgae compared to Corridor 2 (ANOVA, p = 0.0122). Corridor 5 also had significantly lower values for stony corals compared to Corridors 2 and 3 (ANOVA, p = 0.0259). Corridor 3 had significantly higher values for *Palythoa spp.* compared to Corridors 2 and 4 (ANOVA, p = 0.0367).

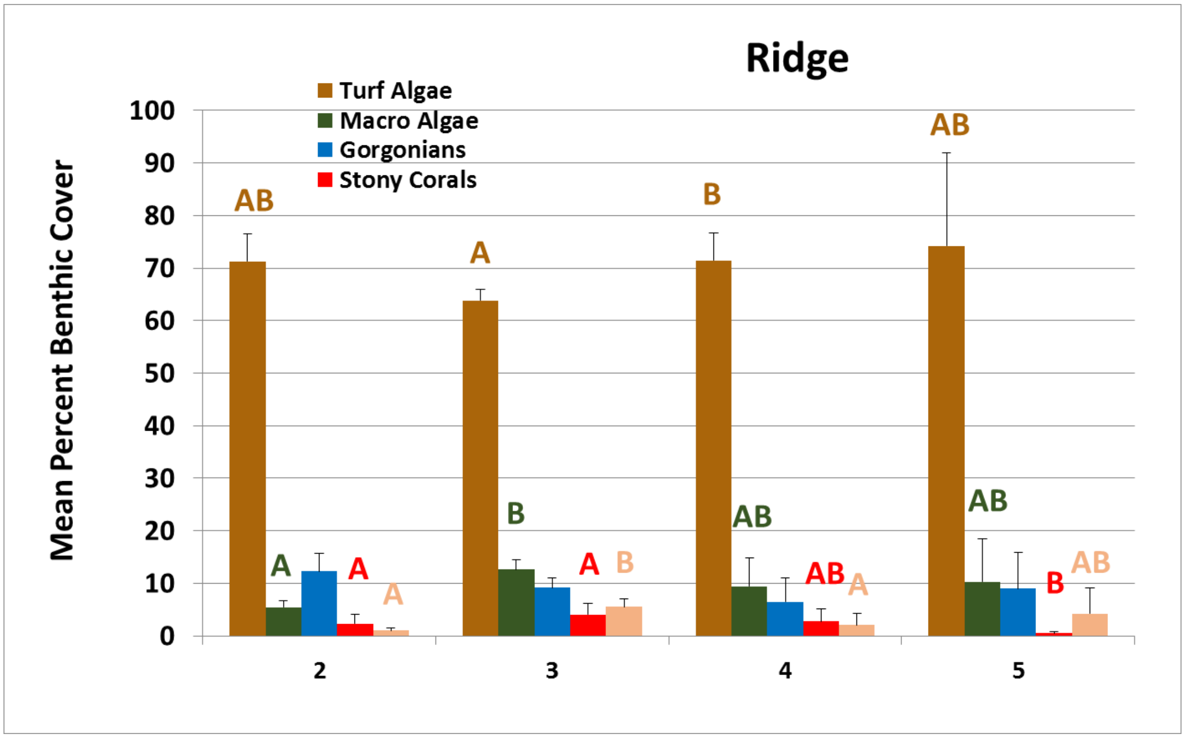
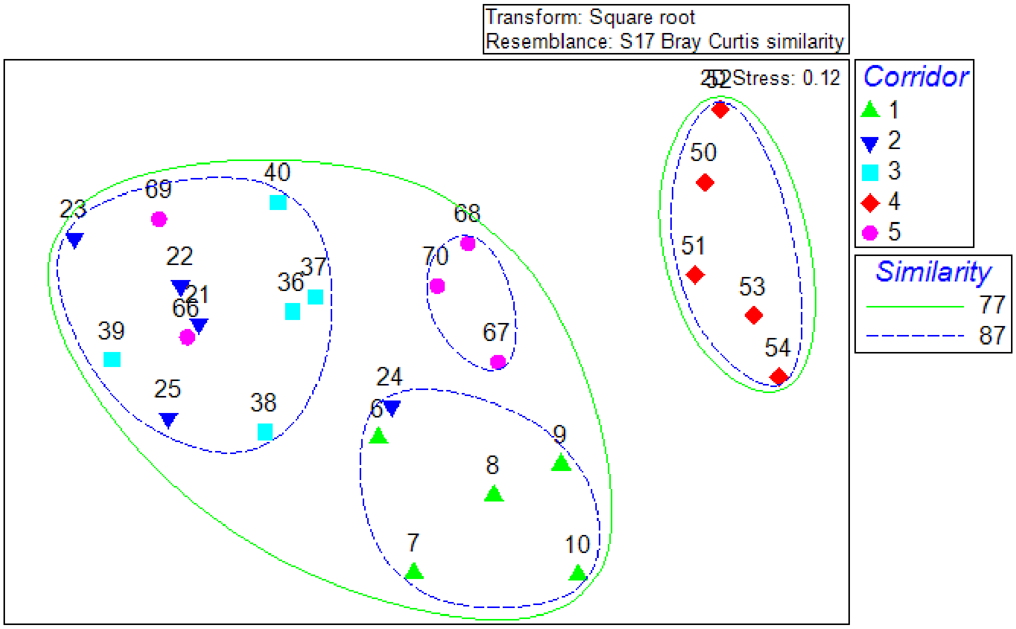


Figure 43. *Mean percent benthic cover for the Ridge by corridor. Corridors, error bars and letters as in Figure 29.*

4.4.9 Inner Reef - Benthic Cover

Corridors 1 and 4 differed significantly from all other Corridors and from each other, while Corridors 2, 3, and, to a lesser extent, 5 clustered together, due to their similar values of macroalgae, sponges, and gorgonians (Figure 44). The SIMPER analyses (based on square-root transformed data) indicated that Corridor 1 differed mainly because of its highest percent cover of stony corals, drastically high gorgonian cover ($\bar{x}$ = 20.35% ± 2.44 SEM) when compared to all other Corridors (Corridor 2: $\bar{x}$ = 10.15% ± 1.52 SEM, Corridor 3: $\bar{x}$ = 10.55% ± 0.93 SEM, Corridor 4: $\bar{x}$ = 5.90% ± 0.81 SEM, Corridor 5: $\bar{x}$ = 7.70% ± 1.35 SEM), and low turf algae values. Corridor 4 had the lowest cover of turf algae, sponge and gorgonians, and the greatest cover of macroalgae and *Palythoa* spp. Of the Corridors that clustered together, Corridor 2 had the highest cover of turf algae and the lowest of macroalgae. Corridor 3 had the lowest *Palythoa* spp. cover. Corridor 5 sites were split into two distinct clusters. The cluster containing sites 67, 68, and 70 reflected their having the highest values of *Palythoa* spp., while sites 66 and 69 had much lower values. Corridor 5 also contained the lowest percent cover of stony corals and the highest cover of sponges. MDS bubble plots (Figure 45) illustrate these differences.



ANOSIM Pairwise Tests	**R Statistic**	**Significance Level %**
Corridor comparison		
1, 2	**0.784**	**0.8**
1, 3	**0.82**	**0.8**
1, 4	**0.964**	**0.8**
1, 5	**0.648**	**0.8**
2, 3	-0.036	52.4
2, 4	**0.992**	**0.8**
2, 5	0.168	11.9
3, 4	**1**	**0.8**
3, 5	0.204	13.5
4, 5	**0.8**	**0.8**

Figure 44. *Inner Reef multivariate analyses results. Top: MDS plot of the Bray-Curtis similarity matrix of the percent benthic cover data of all colonized pavement sites. Outlines represent 77% and 87% similarity from the cluster analysis. Bottom: table summarizes the analysis of similarity (ANOSIM) pairwise test between corridors. Treatments as in Figure 15.*

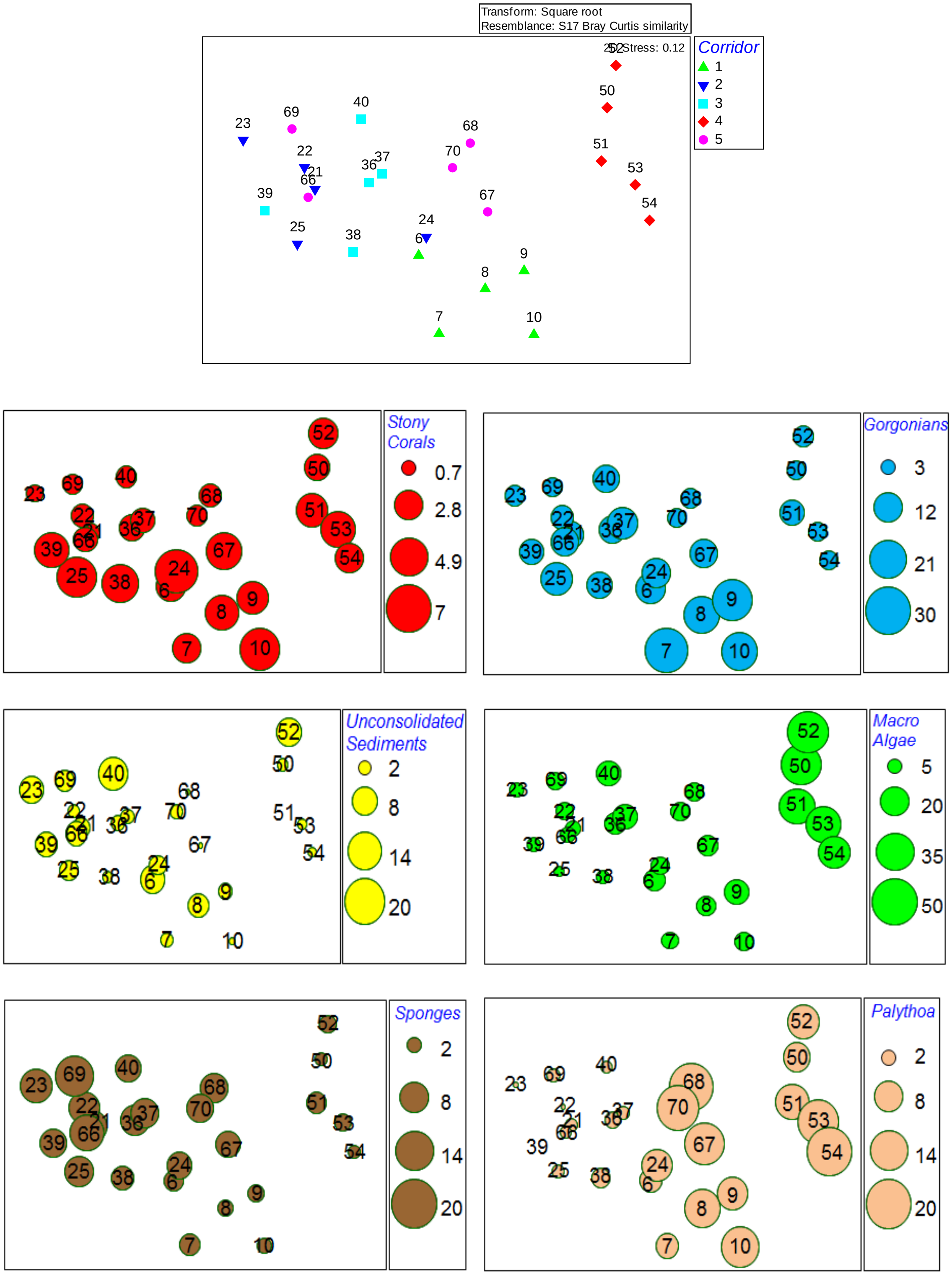


Figure 45. *Inner Reef corresponding 2D bubble plots.*

Figure 46 represents mean percent benthic cover comparisons for the Inner Reef habitat based on untransformed data. Corridor 4 had significantly lower mean percent benthic cover values of turf algae compared to all other Corridors (ANOVA, p = 0.0212). Corridor 1 had significantly lower mean percent benthic cover values of turf algae compared to Corridors 2, 3, and 5 (ANOVA, p = 0.0212). Corridor 4 had significantly higher mean percent benthic cover values of macro algae compared to all other Corridors (ANOVA, p = 0.0122). Corridor 1 had significantly higher mean percent benthic cover values of macro algae compared Corridor 2 (ANOVA, p = 0.0367). Corridor 1 had significantly higher mean percent benthic cover values of gorgonians compared to all other Corridors (ANOVA, p = 0.0216). Corridor 3 had significantly higher mean percent benthic cover values of gorgonians compared to Corridor 4 (ANOVA, p = 0.0212). Corridor 1 had significantly higher mean percent benthic cover values of *Palythoa spp.* compared to Corridors 2 and 3 (ANOVA, p = 0.0356). Corridor 4 also had significantly higher mean percent benthic cover values of *Palythoa spp.* compared to Corridors 2 and 3 (ANOVA, p = 0.0208).

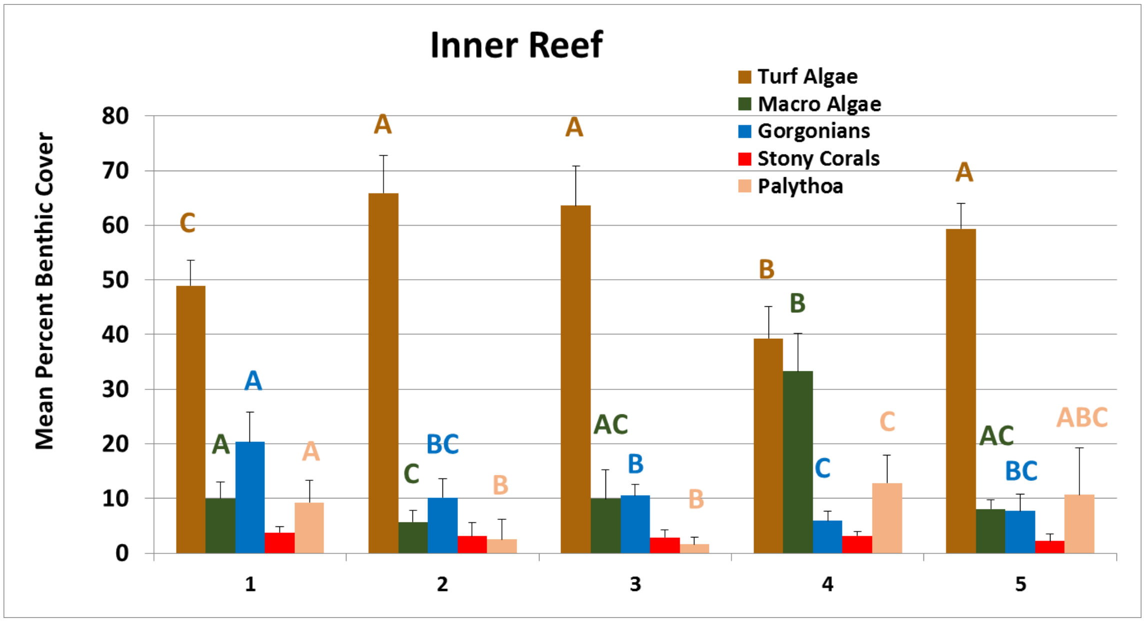


Figure 46. *Mean percent benthic cover for the Inner Reef by corridor. Corridors, error bars and letters as in Figure 29.*

5. DISCUSSION

5.1 Habitat differences

This study found that all corridors exhibited significant differences in percent benthic cover between habitat types, with some differences stronger than others. Both Corridors 1 and 5 exhibited clear differences between all habitat types (Figures 15 and 27). The remaining corridors showed variously weaker differences, as not all habitats were significantly different from each other. However, along Corridor 2, Colonized Pavement sites differed significantly from the Inner Reef and Ridge sites (Figure 18); along Corridor 3, Ridge sites differed significantly from the Colonized Pavement and Inner Reef sites (Figure 21), and, along Corridor 4, Inner Reef sites differed significantly from Colonized Pavement and Ridge sites (Figure 24). Additionally, mean densities of stony corals, gorgonians, and sponges all yielded significant differences between habitats. Across all Corridors, stony coral mean density was significantly greater on the Inner Reef, except Corridor 3 (Figure 9). Within pooled Corridors, gorgonians exhibited many significant differences in mean density across habitat types depending on size class and morphotype. Fans were densest on the Ridge habitat and least dense on the Colonized Pavement (Figure 11). Plumes were significantly denser on the Inner Reef than on either Colonized Pavement or Ridge. Rods were significantly less dense on the Inner Reef. Also, both *Xestospongia muta* and the number of coral colonies infected with *Cliona* spp. occurred at significantly higher mean densities on the Inner Reef relative to the other habitats (Figure 13). Mean species richness of stony corals differed significantly between all habitat types, with the Colonized Pavement having the lowest and Inner Reef the greatest richness values (Figure 10).

In the marine environment, communities are dependent upon many controlling physical factors, including wave exposure, water depth, temperature, turbidity, sedimentation, and light levels. These factors often co-vary, making it difficult to determine which contribute to community differences. On the northern Florida Reef Tract, distinct benthic habitats that house recognizably different communities exist across the shelf with increasing depth (Walker 2012; Walker *et al.* 2008; Walker 2009; Foster *et al.* 2009). Wave exposure drives coral reef distribution through changes in physical disturbance (Denny 1994), sediment flux (Wolanski *et al* 2005), nutrient intake (Hearn *et al.* 2001), and productivity (Dennison and Barnes 1988). A Caribbean-wide study by Williams *et al.* (2015) found that the western Caribbean exhibited the greatest wave exposure and as result, had a significantly different composition of octocorals, dominated by *Antillogorgia americana* and *A. acerosa*, which thrive in areas with high water movement (Yoshioka and Yoshioka 1989). Conversely, sites in the southern Caribbean encountered very low levels of wave exposure and were dominated by the erect branching sponge *Aplysina cauliformis*, which is easily susceptible to breakage from wave disturbance (Wulff 2006). Although wave exposure was not measured in this study, the nearshore habitats (Colonized Pavement and Ridge) average about 1 m shallower than the Inner Reef (Walker 2012), which presumably exposes them to more wave energy. Wave exposure could explain some of the patterns found on the nFRT. For example, gorgonian density may be highest on the Colonized Pavement and Ridge due to increased water movement. Wave exposure might also explain why the largest plumes occurred in higher densities on the Inner Reef. Plume gorgonians such as *A. americana* may have a higher surface area, so that more drag on larger colonies may cause them to dislodge more easily (Sponaugle and LaBarbera 1991). Both the rods and fans had the highest density on the Ridge, while the plume morphotype was highest on the Inner Reef. It is possible that these differences may also be attributed to morphotype preference of wave exposure levels.

Wave exposure can affect sedimentation rates on the reef as well, with intensity likely varying between habitats in different depths. Gilliam *et al.* (2007) used sediment traps to measure sedimentation on all reef tracts in Broward County from 1997 to 2014. Results indicated that the nearshore habitats typically have the highest rate of sedimentation, as well as the largest grain size, followed by the middle and then the outer reef. Jordan *et al.* (2010) measured sedimentation rates off Broward County and found that the deeper Outer Reef study stations exhibited the lowest rates, while the Nearshore Ridge Complex averaged 14 times higher rates. Due to the sea-ward deepening reef profile of the southeastern Florida reef tract (Banks *et al.* 2007; Walker *et al.* 2008), depth and distance from shore showed a strong linear relationship in sedimentation rates (Jordan *et al.* 2010). Coral communities exposed to high turbidity or rapid sedimentation are less diverse and support fewer colonies (Pastorok and Bilyard 1985). The results of this study support this idea, as both coral density and coral species richness increased in deeper habitats further from shore. However, this study did not include data to support or refute this trend continuing to the middle and outer reefs.

Sedimentation rates can also affect coral species composition, as some corals are able to thrive better than others in high-energy habitats. Some corals are less affected by higher amounts of sediment stress than others. Fisher *et al.* (2008) found that, during beach renourishment efforts, *Montastrea cavernosa* became moderately stressed with slight tissue swelling, and remained in this state during eight weeks of post-event analysis, indicating a recovery period to pre-impact levels longer than 8 weeks. This study found *Montastrea cavernosa* to be more abundant in the deeper Inner Reef habitat, containing 64.89% of the colonies found, while the Ridge and Colonized Pavement contained the remaining 25.89% and 9.22%, respectively.

Rugosity affects reef community composition but operates at a comparatively small spatial scale (Williams *et al.* 2015). Rugosity influences species assemblages through an increase in habitable space, as it creates more surface area for organism settlement (Williams *et al.* 2015), while also providing heterogeneous microhabitats (Huston, 1985). Walker *et al.* (2009) determined levels of rugosity for the majority of benthic habitats in the nFRT. Surface-rugosity was acquired from lidar topographic measurements, while linear-rugosity measured *in situ* topographic complexity. Colonized Pavement had both a lower surface-rugosity index and linear-rugosity index (1.003 ± 0.0006 and 1.14 ± 0.01, respectively) than the Ridge (1.004 ± 0.0003 and 1.16 ± 0.01, respectively). Though Walker *et al.* (2009) did not report rugosity values for the Inner Reef, it was visually confirmed during field data collection to have the highest rugosity of the three habitats studied.

Cross-shelf variation is apparent in the fish communities in the Broward-Miami region (Banks *et al.* 2008; Walker *et al.* 2009; Kilfoyle *et al.* 2015). Fish assemblage composition correlates with changes in depth and topographic complexity (Walker *et al.* 2009). Walker *et al.* (2009) found that benthic habitats with the highest mean fish abundances (Linear Reef – Middle, Linear Reef – Outer, and Aggregated Patch Reef) exhibited correspondingly higher values of surface rugosity and volume (with the exception of the Linear Reef Middle – Shallow), while the benthic habitats with the lowest abundances (Colonized Pavement – Shallow and Ridge – Shallow) had the lowest values of elevation, surface rugosity, and volume. In addition to depth and rugosity, other factors influence fish assemblage composition within these habitats, e.g., large storm events and high levels of anthropogenic impacts create a dynamic habitat that houses a high proportion of juveniles subject to annual population fluctuations (Jordan and Spieler 2006), and which helps explain the high community variability within habitats. The nearshore (<300 m from the shore-line) Colonized Pavement fish assemblage particularly shows considerable assemblage differences when compared to the linear reefs, as this low-relief hardbottom supports disproportionately higher densities of juvenile fishes (Lindeman and Snyder 1999; Baron *et al.* 2004; Jordan and Spieler 2006). Studies of developmental patterns suggest that diverse fish species use the nearshore habitats during early life stages as vital nursery grounds and ontogenetically migrate into deeper waters (Vare 1991; Lindeman and Snyder 1999; Baron *et al.* 2004). The high densities of *Acropora cervicornis* located mainly on the shallow Colonized Pavement and Ridge habitats provide shelter for several fish species. In these unique areas, high densities of both juveniles and piscivores have been recorded within the thickets (Gilliam *et al.* 2007). Moving further offshore, Inner Reef sites are dominated by juvenile grunts, whereas wrasses and damselfishes dominate the deeper middle and outer reefs (Jordan *et al.* 2004).

5.2 Latitudinal Variation within Habitats

This study found that all habitat types exhibited significant differences in percent benthic cover between corridors. Among all Colonized Pavement sites (Figure 39), Corridors 1, 3, and 5 were all significantly different from Corridors 2 and 4, and from each other. Figure 38 illustrates the distinct decrease in macroalgae cover and increase in turf algae cover with increasing latitude on the Colonized Pavement. The Ridge sites along Corridors 2, 3, and, to a lesser extent, 5, clustered together, while Corridor 4 sites were spread out (Figure 42) indicating a high level of variability. For the Inner Reef sites, benthic cover on Corridors 1 and 4 differed distinctly from each other and from all other corridors.

Analyses of coral, gorgonian and sponge densities also yielded significant results, but these varied by habitat (Figure 29). Across all habitat types combined, Corridor 1 had the highest mean density of stony corals, though it was not significantly different from that of the other corridors. Nonetheless, it agrees with Walker's (2012) Biscayne Region designation of Corridor 1 and Broward-Miami Region designation of the more northerly Corridors 2-5 (Figure 37). In addition, Corridor 5, the furthest north, had the lowest mean coral density of all corridors, reflecting its close proximity to the boundary of the Deerfield Region identified in the Walker (2012) study. It is possible that low coral density in Corridor 5 could also be due to its close proximity to Hillsboro Inlet.

Mean coral density in all corridors yielded different results when comparing individual habitat types. For instance, on both Colonized Pavement and Ridge sites, Corridors 3 and 4 supported the highest mean coral densities, whereas on the Inner Reef, Corridor 1 mean coral density was significantly higher than in all other corridors. On both Colonized Pavement and Ridge, mean coral species richness was highest in Corridor 3, while the Inner Reef had highest mean coral species richness in Corridor 1. Gorgonian densities varied both latitudinally and by morphotype (Figure 32). Fans on the Colonized Pavement and Ridge sites lacked any clear latitudinal pattern, although they were significantly denser in the northern corridors on the Inner Reef habitat. Plumes on the Colonized Pavement and Ridge sites were denser in the southern Corridors. On the Inner Reef habitat in Corridor 1, mean plume density surpassed mean rod density for the only time during this study. Rods lacked any clear latitudinal pattern within all habitat types. *X. muta* density was significantly lowest on the Inner Reef in Corridor 1, whereas the number of coral colonies infected with *Cliona spp*. had its highest mean density in Corridor 1 on the Inner Reef.

Globally, shallow-water coral communities generally form in a zone extending 30° both north and south of the equator. The northern Florida Reef Tract (FRT) extends from 25 to 27° N, from subtropical southeastern Florida along the coast into a warm temperate environment where tropical reef communities diminish with increasing latitude (Walker and Gilliam 2013), so variation in biological communities is expected. Many parameters change with increasing latitude along this coast, including species richness and evenness (Dodge 1987; Moyer *et al.* 2003, Gilliam 2007; Banks *et al.* 2008; CSA International Inc. 2009). Although this research also found differences between latitudinally-arranged corridors, they were not uniform.

Previously, Walker (2012) and Walker and Gilliam (2013) applied a spatial analysis to identify and quantify specific regions along the coast of southeastern Florida that were statistically distinct in numbers of major benthic habitat types. Evaluation of groupings from a cluster analysis yielded six distinct regions along the coast, beginning with the Biscayne region in the south, followed by the Broward-Miami region, Deerfield region, South Palm Beach region, North Palm Beach region, and the Martin region furthest north. My study was not designed to specifically test community differences between all of these regions, but they were evaluated.

Corridor 1 fell within the Biscayne region, while Corridors 2-5 fell within the Broward-Miami region (Figure 37). Walker (2012) showed the number of benthic habitats decreased with increasing latitude with nine in the southern Biscayne region and four in the North Palm Beach region. Three potential biogeographic barriers were found. The northern Biscayne boundary marked the northernmost extent of oceanic seagrass beds, which this study confirms: Corridor 1 was the only Corridor to contain seagrass in both the habitat mapping and field data collection portions of this study. These seagrass beds, formed by *Thalassia testudinum* and *Syringodium filiforme,* serve a variety of ecological functions, including production of significant fixed organic carbon, sediment stabilization and water baffling (Thorhaug 1981; Lirman and Cropper 2003). Their deep root and rhizome structures reduce erosion in high energy areas (Thorhaug 1981), and they provide habitat, forage, shelter, and nursery grounds for a wide diversity of marine life (Blaber & Blaber 1980; Shulman 1985; Parrish 1989; Laegdsgaard and Johnson 2001).

Corridor 1 had the highest mean coral density and species richness on the Inner Reef, which was significantly further from shore in the Biscayne region (~5 km) than in the Broward-Miami Region (just under 2 km) (Walker 2012). Corridor 1, located further from shore, may have a reduced magnitude of anthropogenic influences than in the more northern Corridors closer to shore. The Inner Reef in the Biscayne region was also ~2 m shallower than in the Broward-Miami region, likely exposing it to higher light intensities that benefit zooxanthellae. These factors may explain at least in part why the Corridor 1 Inner Reef habitat supports the greatest mean coral density and species richness.

Variability among nearshore habitats of the southeastern Florida reef system may result from numerous influencing factors (e.g., temperature, light availability, salinity, seasonality), many of which vary with latitude along the coast near the northern distributional limit of many resident species. Other factors that may limit organism distributions include physical and/or spatial barriers (Pielou 1979; Rapoport 1994; Fraser and Currie 1996; Engle and Summers 1999; Chown and Gaston 2000; Valentine *et al.* 2008). For example, changes in coastal morphologies may generate physical barriers beyond which suitable conditions may not exist for habitat-specific organisms (Walker 2012). In southeastern Florida, the extensive nearshore ridge complex ends at the Hillsboro inlet, drastically reducing or eliminating the organisms of that nearshore habitat further north (Walker 2012).

The tendency for species richness to increase with decreasing latitude has been reported in many studies (Wallace 1878; Dobzhansky 1950; Fischer 1960; Pianka 1966). On the southeast Florida coast, both diversity and abundance of stony coral species on the nearshore hardbottom habitats increase southward from Martin County (Veron 1995; SECREMP 2007; Walker and Gilliam 2013). A synthesis of available reports affirms that

St. Lucie, Martin County, Palm Beach County, and Broward County have 7, 22, 24 and 32 stony coral species, respectively (CSA International Inc. 2009). This pattern was not apparent in this study, as Corridors 1, 2, 3, and 5 all had 17 stony coral species present, while Corridor 4 had 16. This study likely did not capture every species that exists throughout each Corridor, as each site surveyed 60 m^2 without searching elsewhere for additional species. Other surveys using a different methodology would be needed to compare the number of species present within each ecoregion more precisely.

The high mean coral densities in Corridors 3 and 4 might be explained by the fact that 85.14% of all *A. cervicornis* colonies found existed within these corridors. *A. cervicornis* was entirely absent on all habitats on the southern- and northernmost Corridors 1 and 5. This coral was most prevalent on the Colonized Pavement (49.89% of all colonies) and Ridge habitats (44.80%). D'Antonio (2013) found *A. cervicornis* in 39% of 1,428 sites surveyed from Port Everglades to Hillsboro Inlet, in the nearshore environments of southeastern Florida, with high abundances in areas corresponding to Corridors 3 and 4. High-density thickets exist off Broward County (Vargas-Angel *et al.* 2003; Walker *et al.* 2012) including recently discovered populations on the nearshore Ridge complex (Walker and Klug 2014), which show that *A. cervicornis* is able to thrive even in close proximity to highly urbanized coastal features and anthropogenic stressors, including increased freshwater discharge, coastal runoff, sedimentation, sewage effluent, nutrient enrichment, and ship traffic (Thomas *et al.* 2000) from both Port Everglades and the Port of Miami. Such thickets were only found in the Broward-Miami region.

The three most abundant stony coral species found within this study were *Porites astreoides* (29.68% of colonies), *Siderastrea siderea* (17.54%) and *Acropora cervicornis* (10.31%). Stein (2012) recorded similar results. In comparing juvenile versus adult stony coral densities in southeastern Florida, she found that *P. astreoides* had the highest density in the adult coral population in the shallower habitats. Green *et al.* (2008) suggested that the increasing community dominance of *P. astreoides* throughout the Caribbean is being driven by a constant recruitment rate coinciding with reduced percent cover of other coral species. *Porites astreoides* is marked by short longevity (Soong

1991), relatively high fecundity and the production of brooded larvae that typically settle at high densities (Bak and Engel 1979). This species is quite resistant to adverse conditions such as high sedimentation rates (Tomascik 1991) and elevated temperatures (Gates 1990) and typically contains *Symbiodinium* taxa that are hardy with respect to bleaching (LaJeunesse 2002).

Prekel *et al.* (2007, 2008) and Coastal Planning & Engineering, Inc. (2006) recorded 19 stony coral species on the nearshore hardbottom areas of Broward County and found *Siderastrea siderea* to be most common (81.3% of colonies). Goldberg (1973) noted that both *Porites porites* and *Pseudodiploria strigosa* were absent in his limited study of the coral and octocoral communities off southern Palm Beach County. By contrast, *P. porites* accounted for 411 (9.00%) and *P. strigosa* 39 (0.85%) of colonies recorded in the current study. Moyer (2003) also recorded both of these species but included data from the middle and outer reef communities as well. *Acropora palmata*, which is a major reef-building coral located throughout the Caribbean, was not recorded in this study, nor was it found in Goldberg (1973) or Moyer *et al.* (2003). Wirt (2011) however, reported 11 observations located between Biscayne Bay and Martin County on the linear reef and hardbottom habitats. The *Orbicella annularis* species complex (*O. annularies, O. faveolata, and O. franksi*), which typically dominates wider Caribbean reef communities (Knowlton 2001), was uncommon in both the current study and in Moyer *et al.* (2003). Instead, the current study found only 33 *O. faveolata* (0.72% of all colonies) and six *O. annularis* (0.13%) colonies. Laborel (1966) reported a similar lack of *O. annularis* species complex colonies in other high-latitude settings, which has been attributed to the proximity to shore and the deleterious effects of a large human population, which causes high turbidity and decreased light penetration (Goldberg 1973). However, over 50 *O. faveolata* greater than 2 m diameter have been recently found alive in the nearshore habitats of the Broward-Miami region very close to the largest human populations in southeastern Florida (Walker, unpublished).

Montastraea cavernosa, which was the most abundant scleractinian in Moyer *et al.* (2003), accounted for 282 (6.17%) of colonies in this study. Loya (1976) correlated the abundance of *M. cavernosa* with heavy turbidity and sedimentation, and Banks *et al.* (2008) described the southeastern Florida reef environment as turbid. In addition, experimental shading studies found *M. cavernosa* to be more tolerant to reduced light levels than other dominant reef builders such as *O. annularis* complex or *A. cervicornis* (Rogers 1979; Brown and Howard 1985). Burman *et al.* (2012) studied the homogenization of coral assemblages along the Florida Reef Tract. He attributed a greater homogeneity of coral communities across habitats along the Florida Reef Tract to the declines in recent decades of primary reef-building species. Burman *et al.* (2012) supported the idea that today's reefs consist of simpler coral assemblages than in the past and are dominated by eurytopic, generalist species. Though generalists such as *M. cavernosa, Siderastrea* spp., and *Porites* spp. are more stable and therefore more capable of withstanding thermal stress and disease, the Florida Reef Tract has lost the capacity to construct reef framework (Burman *et al.* 2012). This study found an abundance of reef-building *Acropora cervicornis* in the Broward-Miami region, although their capacity to build framework remains unknown due to colony movement (Walker *et al*. 2012).

Stein (in Walker 2012) compared juvenile and adult mean coral densities on the Colonized Pavement, Ridge, Inner Reef, Middle Reef and Outer Reef habitats in the Broward-Miami region, and on the Colonized Pavement and Outer Reef in the Biscayne region. Both Stein (2012) and the current study found lower adult mean coral densities on Colonized Pavement than on the Ridge and Inner Reef, perhaps due to nearshore processes such as wave generated turbidity, sediment transport and sedimentation. However, Stein (2012) found that mean density of adult colonies decreased from the Ridge to the Inner reef, which is in disagreement with the current study, as it found increasing mean density from at least the Ridge to Inner Reef. It is possible that this variability could be due to differences in sample size, as Stein's study had 13 sites (1,170 m^2) in the Broward nearshore habitats, whereas this study included 60 sites (3,600 m^2) in the Broward nearshore study region.

Gorgonians were abundant in almost all habitats and corridors. They may occur at higher densities at higher latitudes than in typical Caribbean reef communities (Moyer *et al.*

2003). Local oceanic circumstances play a role in gorgonian densities and community structure (Moyer *et al.* 2003). Variable weather conditions such as winter storm events produce heavy seas, leading to frequent gorgonian detachment and subsequent mortality (Yoshioka and Yoshioka 1991). Moyer *et al.* (2003) found that the Ridge and Inner Reef habitats located furthest north had lower density and percent cover of gorgonians than the deeper middle and outer reefs, which are less subjected to breaking waves during storms. Corridor 5 agrees with these results, as gorgonian density was conspicuously low on the Colonized Pavement. Conversely, Corridors 2-4 do not agree with these results, as the Colonized Pavement and Ridge habitats both have a higher gorgonian density than the deeper Inner Reef habitat. It is possible that the depth change is not significant enough from the Colonized Pavement to the Inner Reef to recognize similar results found by Moyer *et al.* (2003), as this thesis study did not incorporate data from the Middle and Outer reefs. However, when looking at patterns related to size classes, rod and plume gorgonians in the two largest classes (26 – 50 cm and > 50 cm) had distinctly higher densities in the southern corridors than those in the north.

The nearshore habitats of southeastern Florida provide substrate for the recruitment and growth of many macroalgae species. Macroalgal abundance and diversity can vary substantially with changes in factors such in water clarity, wave energy, and fish and invertebrate grazing pressure (Lobban and Harrison 1994). Differences in macroalgal distribution along the Florida coast are most likely correlated with two major geographical features: 1) the movement offshore of the Gulf Stream to the north, and 2) gradients in seawater temperatures from subtropical to warm temperate latitudes (CSA International Inc. 2009). Macroalgal biomass appears to be relatively higher in the nearshore habitats of the northeastern Florida coast than the southeastern coast (CSA International Inc. 2009). Though this trend has not been explained via experimental testing, it may be due to latitudinal differences in nutrients and wave dynamics (CSA International Inc. 2009). Another explanation could be the relatively higher abundance and diversity of herbivorous fish species in more southern latitudes (Floeter *et al.* 2004). However, in the current study, macroalgal cover on Colonized Pavement decreased with increasing latitude.

Turf-forming algae generally exist in stressful environments such as areas that experience periodic or frequent sedimentation, exposure, and/or high grazing pressure (Airoldi 2001). On the Colonized Pavement habitat, turf algae cover increased with increasing latitude, an inverse pattern to that of macroalgae. These results make sense, when considering wave energy as a factor. Both the Ridge and Inner Reef habitats lacked any strong latitudinal trend in regards to turf and macroalgae cover. However, Corridor 4 on the Inner Reef had a noticeably higher cover of macroalgae and lower abundance of turf algae when compared to the Inner Reef in other corridors. It is curious to note that the Corridor 4 Inner Reef also had the second highest mean coral density, right after the Corridor 1 Inner Reef, located furthest south. Nonetheless, cover of macroalgae can be seasonal and vary over different time scales, so it is possible that the data collected at different times of year would yield different results.

6. CONCLUSIONS

In conclusion, this study showed that differences exist between nearshore habitats both across the shelf and latitudinally off the southeastern Florida coast. The strengths of these differences vary between metrics, habitats, and corridors. This study created a baseline for recognizing local, natural and anthropogenic stressors within the nearshore habitats, while also providing the most recent benthic habitat map of the region and increasing the resolution fourfold from 0.4 ha (1 acre) to 0.1 ha (0.247 acre).

Differences in stony coral, gorgonian, and sponge densities across habitats and latitudes indicated that the habitats were distinct from one another and not homogenous throughout the region. However, these distinctions were not present in all data. Both mean coral density and species richness increased offshore, from the Colonized Pavement to the Inner Reef. Latitudinal trends were not found across corridors, for mean coral density and species richness. As the study area encompassed 68.5 km of coastline, it is possible that this distance was not large enough to capture latitudinal trends in the benthic communities. The three most abundant species were *Porites astreoides, Siderastrea siderea,* and *Acropora cervicornis* which accounted for 57.52% of all coral colonies found. Roughly 95% of *A. cervicornis* colonies were located on either Colonized Pavement or Ridge habitat. Corridors 3 and 4 housed 85.14% of all *A. cervicornis* colonies. Gorgonians were a prominent faunal component in almost all habitats and corridors. Mean gorgonian density was highest on the Ridge and least on the Inner Reef. Rods were most abundant on all habitats, although plumes were more abundant on the Inner Reef than in other habitats, and had a higher mean density than rods on the Inner Reef in Corridor 1. Rod and plume gorgonians in the two largest classes (26 – 50 cm and > 50 cm) had distinctly higher densities in the southern corridors.

Results support the biogeographic regions denoted in the Walker (2012) study as Corridor 1, located in the Biscayne Region, had many statistical differences associated with it. For instance, Corridor 1 Colonized Pavement was the only habitat to contain any seagrass. Also, Corridor 1 Inner Reef habitat had significantly higher values for mean stony coral density, mean stony coral species richness, mean gorgonian density of the plume morphotype, and mean density of corals infected with *Cliona* spp. Corridors 2-4 had some variability associated with them, but were generally similar in benthic composition. Corridor 5, which is in close proximity to the Deerfield Region, also had differences associated with it. Corridor 5 Colonized Pavement and Ridge habitats both had the lowest mean coral species richness, as well as total absence of either sponge species. Corridor 5 Inner Reef was also found to have significantly lower mean stony coral densities compared to Corridors 1, 2, and 4. These results support the idea of different biogeographic regions occurring off the southeastern Florida coast.

In addition to accomplishing the project objectives, this study uncovered new data on the extent of the coral species *Acropora cervicornis* and the existence of ecologically important large coral colonies. These discoveries demonstrate the need for additional research in local nearshore marine habitats off the southeastern Florida coast. The discovery of 110,000 m² of dense patches illuminates a critical data gap in the awareness of *A. cervicornis* distributions and status. Their discovery is so recent that these patches have never been mapped in detail and there is no information on their extent, condition, or distribution. As the condition of these patches cannot be determined from the images, a regional mapping approach is critical in order to determine their health, distribution, and location over time. This is essential for determining when new dense patches form, if they are increasing in number, moving, and/or dissipating through time. The 50 live corals larger than 2 m diameter also deserve considerable attention as they are likely the most resilient colonies in the region given they have persisted for several hundred years and have endured numerous natural and anthropogenic impacts. These corals can be particularly important in the restoration of the reef system, as colony reproductive output increases exponentially with size. These colonies should be monitored and research on their age, fecundity, genetics, and potential restoration applications should be explored.

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