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Shallow-Water Coral Communities Support the Separation of Marine Ecoregions on the West-Central Florida Gulf Coast

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Florida's west coast is a 170,000 km² bedrock shelf (west Florida shelf, WFS) comprised of north-south discontinuous carbonate outcroppings extending more than 200 km from the intertidal zone to a depth of 200 m. These outcrops support diverse benthic communities, which contribute to a multi-billion dollar recreational and commercial fishing industry, yet only about 5% of their extent has been studied in detail. Benthic communities shift over a 6.5° geographic range, but the locations of these shifts are not well-defined. Previous studies have suggested a break in biogeographic regions at Tampa Bay, south at Cape Romano, and north at Cedar Key. The goal of this study was to map and investigate the shallow WFS marine hardbottom north and south of Tampa Bay, FL to identify differences in benthic communities and identify ecoregion boundaries. Habitat mapping yielded 295.89 km² of hardbottom which differed in extent between Sarasota and Pasco counties. Benthic surveys tabulated 4,079 stony coral colonies of nine species and 1,918 soft corals. Stony corals were dominated by *Siderastrea radians*, *Oculina robusta*, *Solenastrea hyades*, and *Cladocora arbuscula* less than 10 cm in diameter. Distinct differences in these communities were evident from south to north. The main community shift indicated an ecoregion boundary at, or very near, the mouth of Tampa Bay. Another shift associated with the Bahamas Fracture Zone (BFZ) occurred at the Pinellas and Pasco County border. The outputs of this work provide the first detailed benthic habitat map of the area, a detailed survey of the composition of hardbottom benthic communities in the region, identify Tampa Bay as a coastal benthic biogeographic transition, and illustrate the influence of the BFZ on coastal communities. These findings illustrate a need for additional WFS benthic research and mapping to give a more comprehensive understanding of coral community biogeography in the context of future warming conditions and the potential tropicalization. Unifying seafloor mapping

data, mapping new areas with high probability of hardbottom resources, and collecting benthic community data over broader scales will refine community biogeographic zonation. This is a necessary precursor to any long-term community monitoring to detect spatial shifts in communities and population modeling.

Keywords: benthic habitat mapping, community characterization, biogeography, west Florida shelf, eastern Gulf of Mexico, Tampa Bay

INTRODUCTION

The Florida-Bahama Platform is ~900 km long extending from 25°N to 30°N (Paull et al., 1990). It covers a broad range of seafloor morphologies, bathymetric gradients, sediment types, benthic biological communities, hardbottom exposures, and reef structures (Hine et al., 2008; Hine and Locker, 2011). There are three southern and central Florida coastal sub-regions that exhibit distinct morphological and oceanographic characteristics from west to east: the west Florida shelf (WFS); the Florida Keys/Dry Tortugas; and the Southeast Florida Coast (Nuttle and Fletcher, 2013). The benthic communities of the Florida Keys/Dry Tortugas and the Southeast Florida Coast have been extensively investigated (Phillips et al., 1990; Hine and Locker, 2011; Walker and Gilliam, 2013; Jaap, 2015), while the WFS communities remain relatively understudied, despite their ecological and economic value (Tchounwou, 1999; Colella et al., 2008; Love et al., 2013; Saul et al., 2013). Estimates show that 50% of the WFS is exposed low relief hardbottom and that only 5% has been studied through detailed surveys (Thompson et al., 1999; Obrochta et al., 2003). These are limited to well-known reef areas (e.g., Pulley Ridge, Florida Middle Grounds, and Steamboat Lumps) or small-scale studies in nearshore habitats (Hine et al., 2003; Hine and Locker, 2011; Baumstark et al., 2016).

The WFS is defined by an expansive bedrock shelf (170,000 km²) that runs from the Florida Panhandle to the lower Florida Keys (Okey et al., 2004). It is comprised of discontinuous carbonate outcroppings that run north and south extending more than 200 km west from the intertidal zone to a depth of 200 m (Okey et al., 2004; Mallinson et al., 2014). The inner continental shelf is separated into three geologic areas: a shallow bedrock sand ridge north of Tampa Bay, a middle ebb-tidal delta, and a southern deep bedrock sand ridge south of Tampa Bay. This underlying bedrock (hardbottom) is common in carbonate and siliclastic marine environments worldwide and consists of ledges that support diverse benthic communities (Hallock et al., 2010; Locker et al., 2016), which contribute to a multi-billion dollar recreational and commercial fishing industry (Okey et al., 2004; Colella et al., 2008; Lirman, 2013).

These hardbottom habitats are shallow (<20 m), with generally turbid waters, and support low diversity mixtures of ahermatypic eurytopic taxa of stony corals (*Cladocora arbuscula*, *Siderastrea* spp., and *Oculina* spp.), octocorals, macroalgae, and sponges (Jaap, 1984; Phillips et al., 1990; Walker et al., 2008; Lirman, 2013). They are classified as essential fish habitat by the NOAA Fisheries serving as nursery and foraging grounds for economically and commercially important species (e.g., grouper, gray snapper, and hogfish) (Jaap, 1984;

Simon and Mahadevan, 1985; Rice and Hunter, 1992; Thompson et al., 1999; Saul et al., 2013; Coleman et al., 2014; Jaap et al., 2014).

West Florida shelf benthic communities tolerate many local stressors that affect the distribution of marine species at various spatial and temporal scales and make corals more susceptible to paling, bleaching, and disease (Dupont and Coy, 2008; Anderson, 2009; Asis et al., 2017). A few of the common stressors are water temperature, hurricane and storm surges, river discharge, and harmful algal blooms (HABs).

Coastal water temperatures on the WFS vary from 18 to 30°C, but can drop below 10°C (Mallinson et al., 2014; Locker et al., 2016; Klaus et al., 2017), which can increase stress and cause mortality events (Klaus et al., 2017; Overstreet and Hawkins, 2017).

The WFS is typically a low energy environment with tidal ranges <1 m, however, it is frequently affected by hurricane and tropical storm surges (Hallock et al., 2010; Locker et al., 2016). Hurricanes and storm surges can cause large shifts in sediment that can smother the local biota including corals, gorgonians and sponges (Anderson, 2009), or expose areas previously covered in sediment. These natural events lead to spatial shifts in distribution and succession of benthic communities and fragmentation of benthic habitats (Briones, 2004).

Proximity of benthic communities to rivers, estuaries, and bays influences abundance, biomass, and community composition of the benthos by many environmental factors including salinity, turbidity, temperature, and nutrients (Briones, 2004). Excessive flow of nutrients can arise from major river systems and impact the water quality which can exacerbate HABs (Briones, 2004; Colella et al., 2008) and may cause large-scale community shifts depending on their intensity and frequency (Overstreet and Hawkins, 2017). Over the last few decades, HABs have affected coastal communities across increasing geographic areas, threatening the health of humans and causing large-scale mortality of marine organisms, including benthic communities (Colella et al., 2008; Anderson, 2009). The nearshore oligotrophic waters of the WFS are defined by a long residence time increasing their susceptibility to stratification that can favor development of phytoplankton blooms (Nuttle and Fletcher, 2013; Weisberg et al., 2016). More than 40 species of toxic microalgae live naturally in these waters at low concentrations. While red tides or algal blooms are a natural phenomenon, they can be exacerbated by human activities, pollution, and heavy outflow of major river systems into the Gulf (Anderson, 2009; Overstreet and Hawkins, 2017). The most common HABs in the Gulf of Mexico consist of the dinoflagellate *Karenia brevis*, and have occurred nearly annually on the west Florida coast since the mid-1980s. When concentrations of *K. brevis* are high, brevetoxin, a compound

within the dinoflagellate, can cause massive fish kills, paralytic shellfish poisoning, and if persistent, large-scale mortality of marine organisms (Colella et al., 2008).

There is a climate gradient along the Florida peninsula ranging from warm-temperate in the north to sub-tropical in the south, causing evident latitudinal changes in marine hardbottom communities (Engle and Summers, 2000; Spalding et al., 2007; Walker et al., 2008; Canning-Clode, 2009; Walker and Gilliam, 2013; Toonen et al., 2016). Three marine biogeographic ecoregions have been identified along Florida's coast as described in "Marine Ecoregions of the World"; a hierarchical system based on taxonomic configurations, influenced by evolutionary history, patterns of dispersal, and isolation (Spalding et al., 2007) (**Figure 1**). This volume identified a split between the Northern Gulf of Mexico and Floridian ecoregions just north of Tampa Bay. Similarly, the Environmental Monitoring and Assessment Program for Estuaries (EMAP-E) used climate and ocean currents to delineate Florida into Carolinian (Virginia to St. Lucie Inlet, FL, United States), West Indian (St. Lucie/Jupiter Inlet to Tampa Bay, FL, United States), and Louisianian provinces (Tampa Bay, FL, United States through the Texas border) (Engle and Summers, 2000). The West Indian and Louisianian provinces split the northern Gulf of Mexico inhabiting warm-temperate waters just north of Tampa Bay, FL from the more tropical waters of the southern WFS (Engle and Summers, 2000).

However, there is inconsistency as to where biogeographic transitions are located. Many coastal and shallow habitats base these boundaries on taxonomic distributions and percent endemism within a geographic boundary (Briggs and Bowen, 2012). Boundaries are often fuzzy and vary with different seasonal temperatures and are typically defined by fish distributions due to unavailable or incomplete benthic community data (Engle and Summers, 2000; Toonen et al., 2016). On the WFS, benthic communities shift over a 6.5° geographic range from the Florida Keys to northern Florida (Hine and Locker, 2011), but the location of these shifts are not quantified or well-defined. Previous studies have suggested a break in biogeographic regions at Tampa Bay, south at Cape Romano, and north at Cedar Key (Engle and Summers, 2000; Toonen et al., 2016). Other studies suggest that the west central coast resides in a second part of the Carolinian province (Briggs and Bowen, 2012; Toonen et al., 2016). These are important to identify now more than ever. As the climate continues to warm, many have proposed the poleward tropicalization of temperate environments (Verges et al., 2014) and in some cases, these are occurring now (Yamano et al., 2011). Community biogeographic baseline data are essential in order to detect tropicalization effects.

Benthic habitat maps can be used to define reef community biogeography (Walker, 2012; Fisco, 2016; Ames, 2017). Habitat mapping of the Florida Reef Tract (FRT) on Florida's Atlantic coast has provided accurate maps and habitat characterization for 955 km² of shallow (<40 m) seafloor. Quantitative analyses of the community and habitat data supported the designation of seven distinct ecoregions over 10's of km spatial scale identifying biogeographic boundaries in southeast Florida (Walker, 2012; Walker and Gilliam, 2013; Walker and Klug, 2014). There was an overall reduction in community diversity from south to the

north changing significantly at the Bahamas Fracture Zone (BFZ) that functions as a divide of sub-tropical and temperate waters on the SE FRT (Walker and Gilliam, 2013). Habitat mapping on the WFS could be used similarly if it existed.

While latitudinal variations in benthic habitats (Walker, 2012), benthic communities (Walker and Gilliam, 2013; Klug, 2015), and reef fish (Fisco, 2016; Ames, 2017) support the definition of separate coral reef ecosystem ecoregions on the FRT, the WFS remains understudied and benthic marine community spatial differences have yet to be quantitatively investigated. Thus, the goal of this study was to map and investigate the WFS marine hardbottom north (Pasco and Pinellas counties) and south (Sarasota County) of Tampa Bay, FL to identify differences in benthic communities and the potential for ecoregion categorization. We identify latitudinal changes in the hardbottom community composition and where those changes occur. Our objectives were to (1) construct a benthic habitat map of approximately 1,200 km² of shallow-water seafloor north and south of Tampa Bay, (2) collect quantitative survey data to characterize hardbottom benthic communities across the map, and (3) investigate coastal benthic community spatial patterns in a biogeographic context. The outputs of this work provide the first detailed benthic habitat map of the area, a detailed survey of the composition of hardbottom benthic communities in the region, identify Tampa Bay as a coastal benthic biogeographic transition, and illustrate the influence of the BFZ on coastal communities.

MATERIALS AND METHODS

Benthic Habitat Mapping

Archived WorldView-2 (WV2) and QuickBird (QB) source imagery taken between December 2nd, 2011 and June 27th, 2016 of optically shallow water areas (0–20 m) were used for benthic habitat mapping. Study areas (**Figure 1**) were chosen based on locations where archived satellite imagery was suitable for visual image interpretation (mapping). Detailed habitat mapping of the imagery was accomplished by visual interpretation at a 1:3,000 scale with a minimum mapping unit of 0.4 ha (1 acre) following similar methodologies used by other regional mapping efforts (Walker et al., 2008; Walker and Gilliam, 2013). Features were classified to the Florida Unified Reef Map following the Federal Coastal and Marine Ecological Classification Standard (CMECS). CMECS was used for habitat categorization and was modified where necessary to better define habitats. Groundtruth video data were collected at 258 locations throughout the study area in August 2016 and March 2017 using drop cameras to visualize and determine habitat type in each location. The video data were used to inform the image interpretation process in GIS.

Community Composition Data Collection

Mapped hardbottom habitats were sampled to determine benthic community composition and its present condition. Twenty-nine haphazardly chosen, shallow-water (<20 m) hardbottom quantitative survey sites (**Figures 2, 3**) were visited over a 6-day period between July 17 and 22, 2017; 15 in the northern mapped

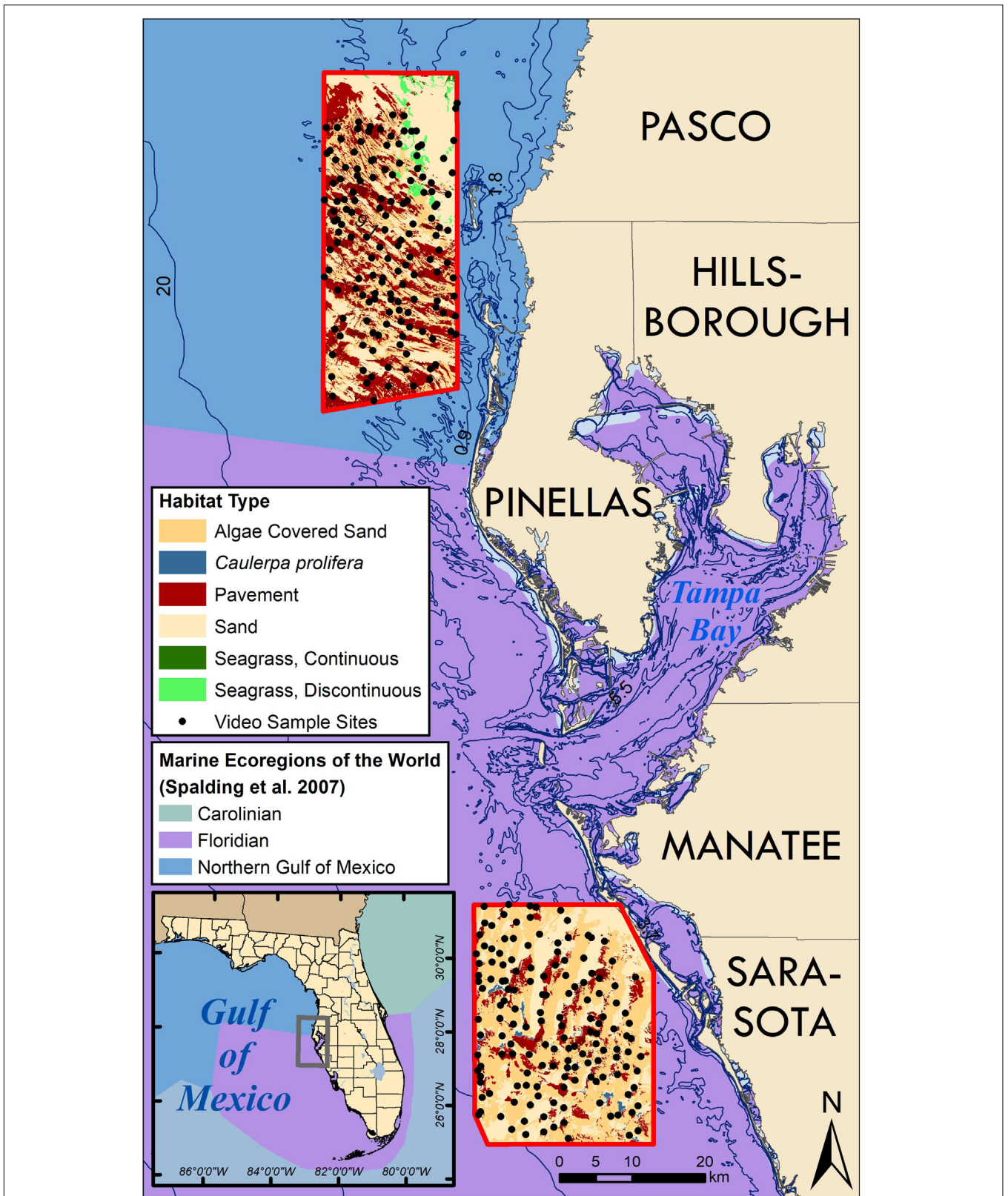


FIGURE 1 | A map of west coastal Florida near Tampa Bay illustrating the benthic habitat maps (bordered in red) where groundtruthing video was collected to confirm habitat type (black dots). Adjacent counties are labeled. Ocean colors on main map and inset (lower left) represent the Marine ecosystems of the World from Spalding et al. (2007). The transition between Florida and Northern Gulf of Mexico is located just north of Tampa Bay.

area and nine in the south. The mapping attempted to distinguish high biological covered pavement by delineating the darkest portions of the habitat in the imagery separately, assuming the dark coloration was from denser cover. Thus, one pavement and one pavement-high cover (biological) site were haphazardly selected near randomly chosen map locations, utilizing a random design but also allowed comparison between the two cover types at each location.

At each site, four non-overlapping 20 m transect tapes parallel to each other were extended without crossing into a different habitat. Photographs were collected 52 cm above the surface at 1-m intervals along the length of each transect. Simultaneously, a 1-m belt survey was conducted along 15 m of the two middle transects (30 m² total) to document coral demographic and condition data. Along each of the middle transects, scleractinian corals greater than 4 cm were identified, counted, and measured (max length, width, and height) to calculate density. Gorgonian coral density was binned into height size classes (4–10, 11–25, 26–50, 50+ cm) and by individual morpho-type (Rod, Plume, and Fan). Percent mortality and the presence and severity of bleaching and disease were documented for each coral surveyed. Bleaching and disease prevalence were tabulated by the number of affected colonies divided by the total number of colonies.

Percent cover was estimated from the transect photographs using Coral Point Count with excel extensions (CPCe) software (Kohler and Gill, 2006). Twenty randomly placed points were assigned on each image where the substrate and organisms were identified to functional groups using a specially designed source code with known shallow WFS species. Algae were identified to their most general taxonomic level (i.e., Red algae, Brown Algae, and Green Algae), and corals were identified to their lowest taxonomic level (i.e., family and species).

Statistical analyses of the benthic community data included non-parametric analysis of variance (ANOVA) to examine differences in major functional group cover, abundances, species richness, number of diseased colonies, percent live tissue, and percent of recent dead. Non-metric, multidimensional scaling (MDS) plots were constructed using Bray-Curtis similarity indices to examine differences in community structure (PRIMER v6). An analysis of similarity (ANOSIM) test was used to identify differences in community structure, and similarity percentage (SIMPER) analysis was used to identify those species most responsible for the differences seen among different factor groups. All data underwent a thorough process of quality assurance and quality control before and after being compiled and statistically analyzed. Datasheets were reviewed for consistency and clarification. Any outlier species identifications or abundance/sizes etc. were reviewed and changed when appropriate.

RESULTS

Satellite Image Mapping

A total mapped area of 1,263.34 km² total seafloor indicated 23.4% (295.89 km²) of the surveyed cover was pavement and 76.6% (967.45 km²) was sand. Pavement was originally

divided into two categories pavement, and pavement-high cover (biological), but the similarity between pavement and pavement-high cover sites suggested that the map did not distinguish pavement by cover very well. Therefore, we combined these classes into one class called pavement. Sand was categorized into several categories based on biological cover. Of the total mapped area, 40% (505.51 km²) was sand covered with cyanobacteria, while 34.6% (437.25 km²) consisted of bare sand, 0.4% (4.56 km²) was sand with *Caulerpa prolifera*, and 1.6% (20.13 km²) was sand with seagrass (Table 1).

Habitat distribution differed between the north and south study areas (Table 1). The northern study area contained 72.9% (215.77 km²) of the total pavement, 100% (20.13 km²) of continuous and discontinuous seagrass, and 37.3% (188.56 km²) of sand-cyanobacteria (Figure 2). The southern study area contained 27.1% (80.12 km²) of the pavement, 100% (4.56 km²) of the *Ca. prolifera*, and 62.7% (316.95 km²) of the sand-cyanobacteria (Figure 3).

The habitats also varied within each mapped area (Table 1). The northern area was comprised of 33.5% pavement, 34% (218.77 km²) sand, 3.1% continuous and discontinuous seagrass, and 29.3% sand-cyanobacteria. The southern area was comprised of 12.9% pavement, 35.2% (218.48 km²) sand, 0.7% sand-*Ca. prolifera*, and 51.1% sand-cyanobacteria.

Benthic Communities

Stony Corals

Florida's west coast hardbottom shelf contains a vast and dense community of ahermatypic stony corals, albeit less diverse than further south. A total of 4,079 stony coral colonies were identified and measured in this study (Table 2). Ten species were identified, however, four species [*Siderastrea* spp. (42.46%), *Oculina robusta* (28.61%), *Solenastrea hyades* (21.52%), and *Cl. arbuscula* (6.33%)] comprised 99.92% of the total stony corals measured in this study. Total mean density of stony corals (colony m⁻²) was high, 11.56 corals m⁻², compared to a mean density of 6.68 ± 0.35 colonies m⁻² on the SE FRT (Gilliam et al., 2017). Sarasota County had the highest mean density of corals (18.4 m⁻²), where Pasco County had the lowest mean density (5.18 m⁻²) and Pinellas County had a moderate mean density (11.42 m⁻²). *Siderastrea* spp. had the highest density (4.90 m⁻²) followed by *O. robusta* (3.30 m⁻²), *So. hyades* (2.48 m⁻²), and *Cl. arbuscula* (0.73 m⁻²) (Table 2).

No large tropical reef-building corals were found in this study. Stony corals were found in very high densities but consisted of small individuals (<40 cm). Seventy-three percent of coral colonies were less than 10 cm long and 80% of these corals were less than 10 cm tall. There was a mean coral size in Sarasota County of 9.12 cm (± 0.32 SE) length, 7.83 cm (± 0.85 SE) width, and 7.98 cm (± 1.16 SE) height. The mean coral size in Pinellas County was 5.42 cm (± 0.14 SE) length, 3.92 cm (± 0.14 SE) width, and 3.75 cm (± 0.16 SE) height. The mean coral size in Pasco County was 7.95 cm (± 0.51 SE) length, 6.54 cm (± 0.47 SE) width, and 5.93 cm (± 0.35 SE) height. The fire coral species *Millepora complanata* had the largest length, width, and height of the species surveyed (>30 cm) due to its encrusting nature.

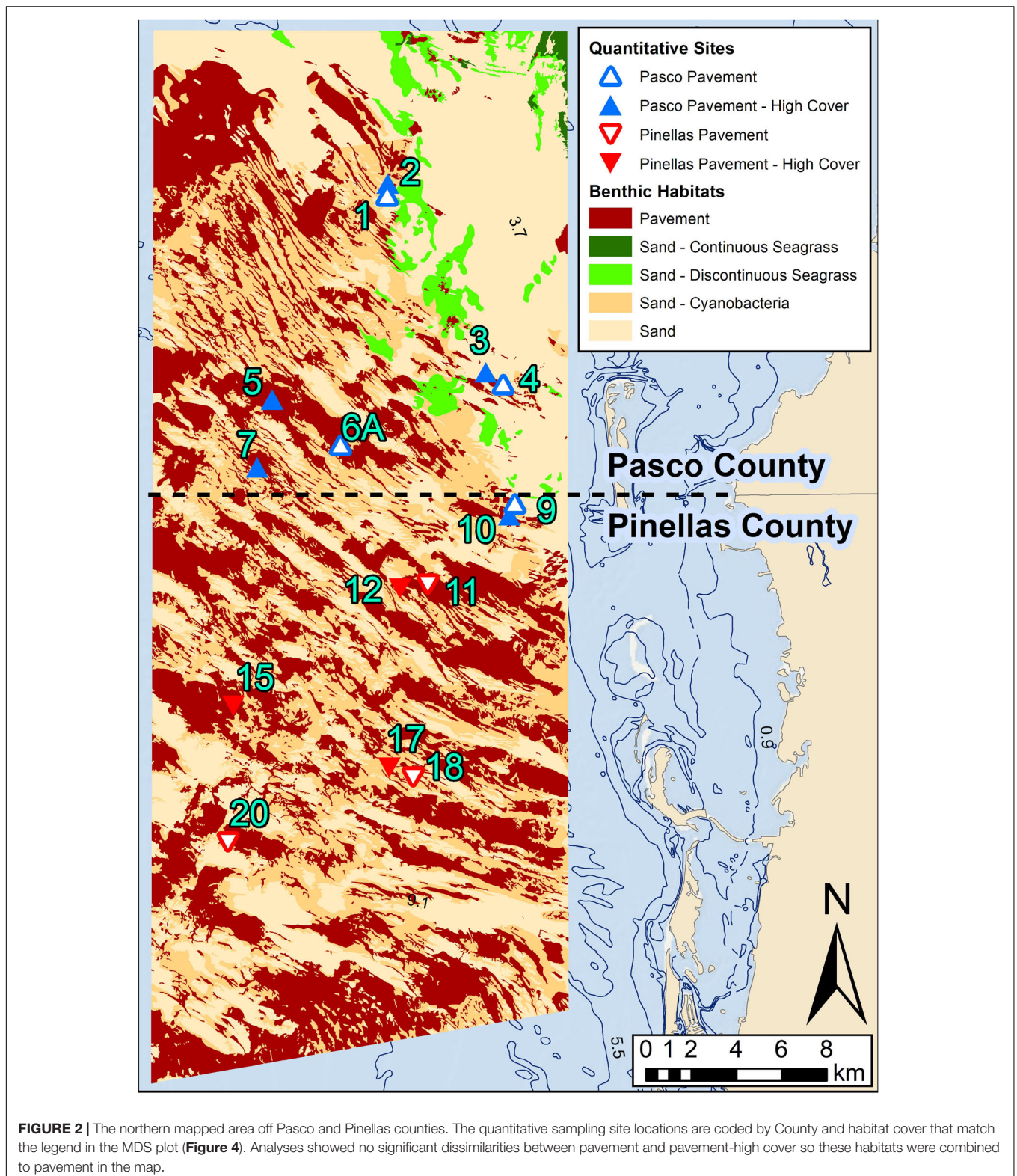


FIGURE 2 | The northern mapped area off Pasco and Pinellas counties. The quantitative sampling site locations are coded by County and habitat cover that match the legend in the MDS plot (**Figure 4**). Analyses showed no significant dissimilarities between pavement and pavement-high cover so these habitats were combined to pavement in the map.

Out of the ten coral species documented, only four species (*Siderastrea* spp., *O. robusta*, *So. hyades*, and *Cl. arbuscula*) showed signs of disease, paling, partial bleaching, or bleaching,

totaling 838 of 4,079 individuals (**Table 3**). This equated to 19% of the corals exhibiting at least some stress condition, however this varied dramatically by species. *O. robusta* had

TABLE 1 | Area (km²) table of benthic habitats by location.

Habitats area (km ²)	North	South	Total	% of total
Pavement	215.77	80.12	295.89	23.4%
Sand	218.77	218.48	437.25	34.6%
Sand – Continuous seagrass	2.79	0	2.79	0.2%
Sand – Discontinuous seagrass	17.34	0	17.34	1.4%
Sand – <i>Caulerpa prolifera</i>	0	4.56	4.56	0.4%
Sand – Cyanobacteria	188.56	316.95	505.51	40%
Grand total	643.22	620.11	1,263.34	100%

a 51.8% bleaching prevalence (combining partially and totally bleached) whereas 17.1% of *So. hyades*, 2.3% of *Cl. arbuscula*, and 0.8% of *Siderastrea* spp. were bleached. Over 85% of bleaching occurred on *O. robusta* (586) and *So. hyades* (129). These two-species had the highest amount of paling, partial bleaching, and bleaching documented. Total disease prevalence was extremely low (0.1%) and was documented in only two species, *Siderastrea* spp. (0.23%) and *So. hyades* (0.23%). The type of disease was not identified or confirmed.

Gorgonians

Gorgonians were very abundant, with a total count of 1,918 colonies (Table 4). Total mean density of gorgonians was 5.43 ± 0.46 SE m⁻². Sarasota County had the highest mean density of gorgonians (12.13 ± 7.1 SE m⁻²), Pasco County had the second highest mean density of gorgonians (2.01 ± 0.42 SE m⁻²), and Pinellas had the lowest mean density of gorgonians (0.12 ± 0.21 SE m⁻²). The dominant morpho-type was rods, which comprised 67.2% of the gorgonians counted. These were dominated by two size classes; Rods 11–25 cm and Rods 26–50 cm. Plumes comprised 32.8% of the gorgonian individuals recorded and were dominated by Plume 26–50 cm and Plume 50+ cm size classes. Only one Fan 26–50 cm was recorded. No bleaching or diseased gorgonians were found.

Community Spatial Patterns

Region

The community analyses suggest that the benthic communities in the south (Sarasota County) were very different from the north sites (Pinellas and Pasco counties). The average dissimilarity between the Northern and Southern sites was 53.16% and an ANOSIM test was significant ($p = 0.1$, $R = 0.431$). Differences between regions were driven by stony coral and gorgonian metrics. Mean density of *So. hyades* (N: 0.80 ± 0.19 SE, S: 5.21 ± 0.94 SE) and *Siderastrea* spp. (N: 3.20 ± 0.67 SE, S: 7.84 ± 1.47 SE) were significantly different between Northern and Southern sites (SHYA: ANOVA, $p = 0.001$; SID spp: ANOVA, $p = 0.006$).

Regional differences between gorgonian morpho-type and colony size classes were observed. Mean density of Rod morpho-type was significantly different between the size class 4–10 cm (N: 0.12 ± 0.03 SE, S: 0.85 ± 0.48 SE) (ANOVA, p -value = 0.027) and 50+ cm (N: 0.09 ± 0.02 , S: 1.33 ± 1.07 SE) (ANOVA, $p = 0.009$). Plume morpho-type mean density was significantly different between regions for size classes 4–10 cm (ANOVA, $p < 0.001$) and 11–25 (ANOVA, $p < 0.001$). South sites had a

significantly higher mean density of Plume 26–50 cm (1.47 ± 1.19 SE) than the North (0.01 ± 0.01 SE) (ANOVA, $p = 0.003$).

There were few significant differences in percent cover of biota between the North and South. Hardbottom veneered with sediment cover was higher in the north (N: 43.84%; S: 20.65%) (ANOVA, $p = 0.009$) and exposed Hardbottom cover was higher in the south (N: 19.27%; S: 39.53%) (ANOVA, $p = 0.023$). Brown Algae cover was significantly higher in the north (N: 10.97%; S: 2.25%) (ANOVA, $p < 0.001$) and Plume gorgonians (N: 0.24%; S: 3.30%) were significantly higher in the south (ANOVA, $p = 0.013$).

County

Multivariate analyses of density data (stony coral species and gorgonian morpho-type by size class) showed distinct spatial patterns among counties (Figure 4). The northern most sites in Pasco County (blue triangles in Figure 4) were 64.7% similar, Pinellas County (red triangles) sites were 65.6% similar, and the southern Sarasota sites (green squares) were 54.1% similar; all clustering in groups and in spatial order. Pasco and Pinellas had an average dissimilarity of 42.5%. Pasco and Sarasota had an average dissimilarity of 54.5%. Pinellas and Sarasota sites had an average dissimilarity of 51.2%. An ANOSIM statistically supported the County differences in benthic community density with the strongest difference between Pasco and Sarasota sites ($R = 0.512$). A 3-dimensional bootstrap averages plot clearly illustrates the statistical dissimilarity in coral densities on pavement sites between counties (Figure 5).

A Pearson correlation overlaying the MDS showed the major contributors of the spatial patterns in the data (Figure 4). Mean stony coral density increased significantly by County from north to south with the lowest in Pasco County sites (5.18 ± 0.23 SE m⁻²), then Pinellas County sites (11.42 ± 0.60 SE m⁻²), and Sarasota County sites (18.4 ± 0.86 SE m⁻²) (Figure 6). Differences were mostly driven by *Siderastrea* spp., *O. robusta*, and *So. hyades* (Figure 7). The mean density of *Siderastrea* spp. was $1.76 (\pm 0.38$ SE m⁻²) in Pasco sites, $5.35 (\pm 1.10$ SE m⁻²) in Pinellas, and $7.84 (\pm 1.50$ SE m⁻²) in Sarasota sites (ANOVA, p -value = 0.012). The mean density of *So. hyades* was $0.67 (\pm 0.16$ SE m⁻²) in Pasco sites, $1.00 (\pm 0.40$ SE m⁻²) in Pinellas sites, and $5.21 (\pm 0.94$ SE m⁻²) in Sarasota sites (ANOVA, p -value = 0.005). Sarasota County sites had the highest densities of all stony corals except *Cl. arbuscula*, which was higher in both Pasco and Pinellas sites.

Gorgonian densities varied between counties as well (Figure 6). Sarasota had the highest total mean gorgonian density (12.13 ± 1.00 SE m⁻²) (ANOVA, $p = 0.006$). Pasco had the second highest mean density (2.01 ± 0.18 SE m⁻²) and Pinellas had the lowest (0.13 ± 0.02 SE m⁻²). Gorgonian density in Sarasota was comparable to the mean density in the FL Keys (12.96 ± 0.59 SE colonies m⁻²) (Smith et al., 2011).

Most of the recorded gorgonians were greater than 10 cm (84.6%). Sarasota had significantly higher (ANOVA, $p = 0.014$) density of gorgonians greater than 10 cm (10.06 ± 4.1 SE m⁻²) than Pinellas County (0.13 ± 0.05 SE m⁻²) and higher densities of gorgonians less than 10 cm (2.07 ± 0.05 SE m⁻²) than Pinellas (ANOVA, $p = 0.004$).

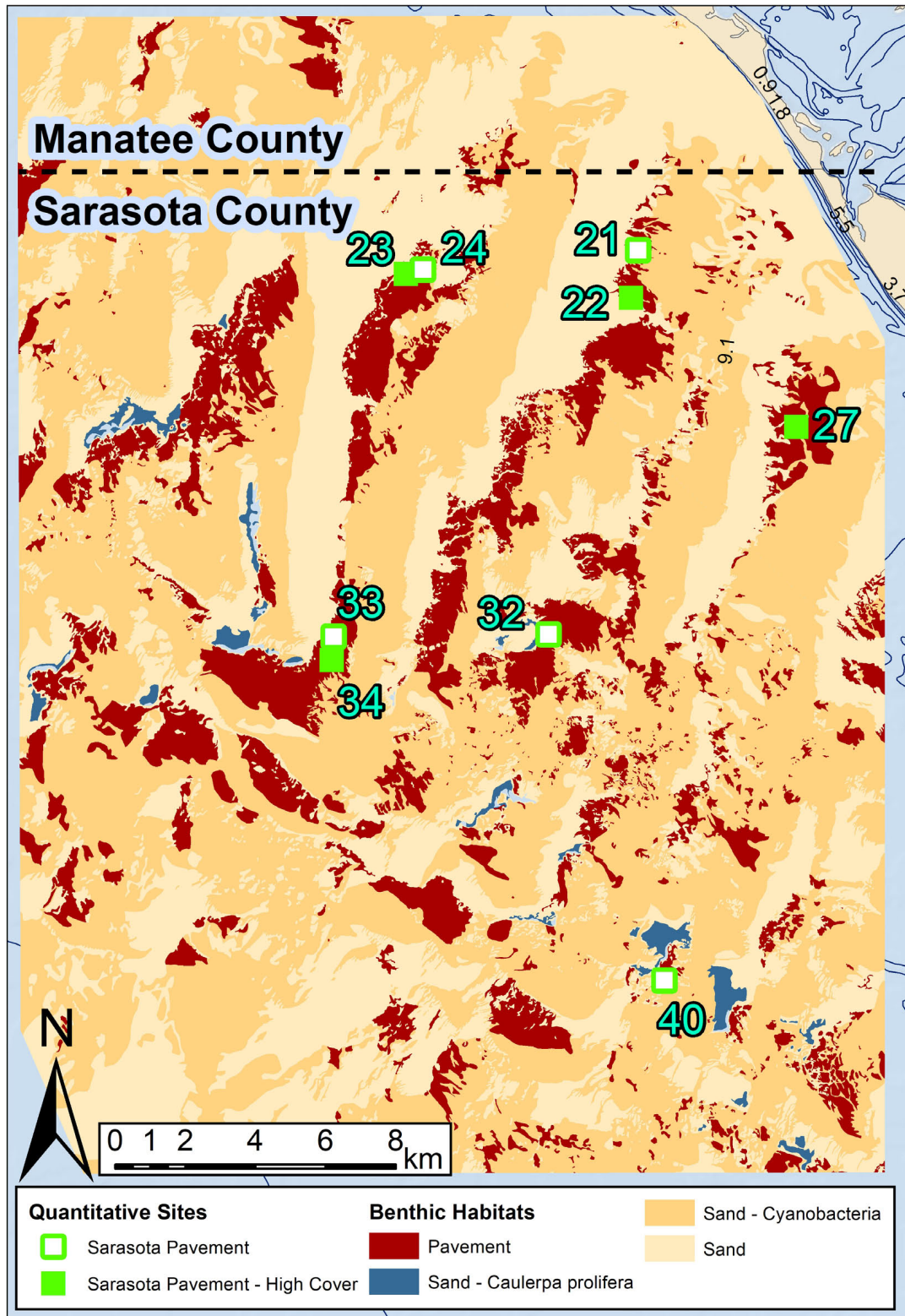


FIGURE 3 | The southern mapped area of Sarasota County. The quantitative sampling site locations coded are coded by County and habitat cover that match the legend in the MDS plot (Figure 4). Analyses showed no significant dissimilarities between pavement and pavement-high cover so these habitats were combined to pavement in the map.

TABLE 2 | Stony coral species, abundance, and density per m² of corals observed, sorted by county.

Species	Pasco		Pinellas		Sarasota	
	Abundance	Density per m ²	Abundance	Density per m ²	Abundance	Density per m ²
<i>Siderastrea</i> spp.	238	1.76	441	5.35	1,059	7.80
<i>Oculina robusta</i>	256	1.90	306	4.28	605	4.48
<i>Solenastrea hyades</i>	90	0.67	85	1.00	703	5.21
<i>Cladocora arbuscula</i>	108	0.80	57	0.70	93	0.69
<i>Stephanocoenia intercepta</i>	2	0.01	1	0.01	18	0.13
<i>Manicina areolata</i>	3	0.02	6	0.08	0	0.00
<i>Porites divaricata</i>	0	0.00	0	0.00	5	0.04
<i>Millepora complanata</i>	2	0.01	0	0.00	0	0.00
<i>Millepora alcornis</i>	0	0.00	0	0.00	1	0.01
Pooled total	699	5.18	896	11.42	2,484	18.40
Overall total	4079	11.56				

TABLE 3 | Condition (bleaching and disease) of the stony corals observed in the benthic quadrat surveys with bleaching and disease prevalence by species.

Species	Diseased	Pale	Partially bleached	Bleached	Bleaching prevalence	Disease prevalence
<i>Siderastrea</i> spp.	4	14	14	0	0.80%	0.23%
<i>Oculina robusta</i>	0	22	586	18	51.80%	0%
<i>Solenastrea hyades</i>	2	21	129	21	17.10%	0.23%
<i>Cladocora arbuscula</i>	0	1	6	0	2.30%	0%
Grand total	6	58	735	39	19.00%	0.15%

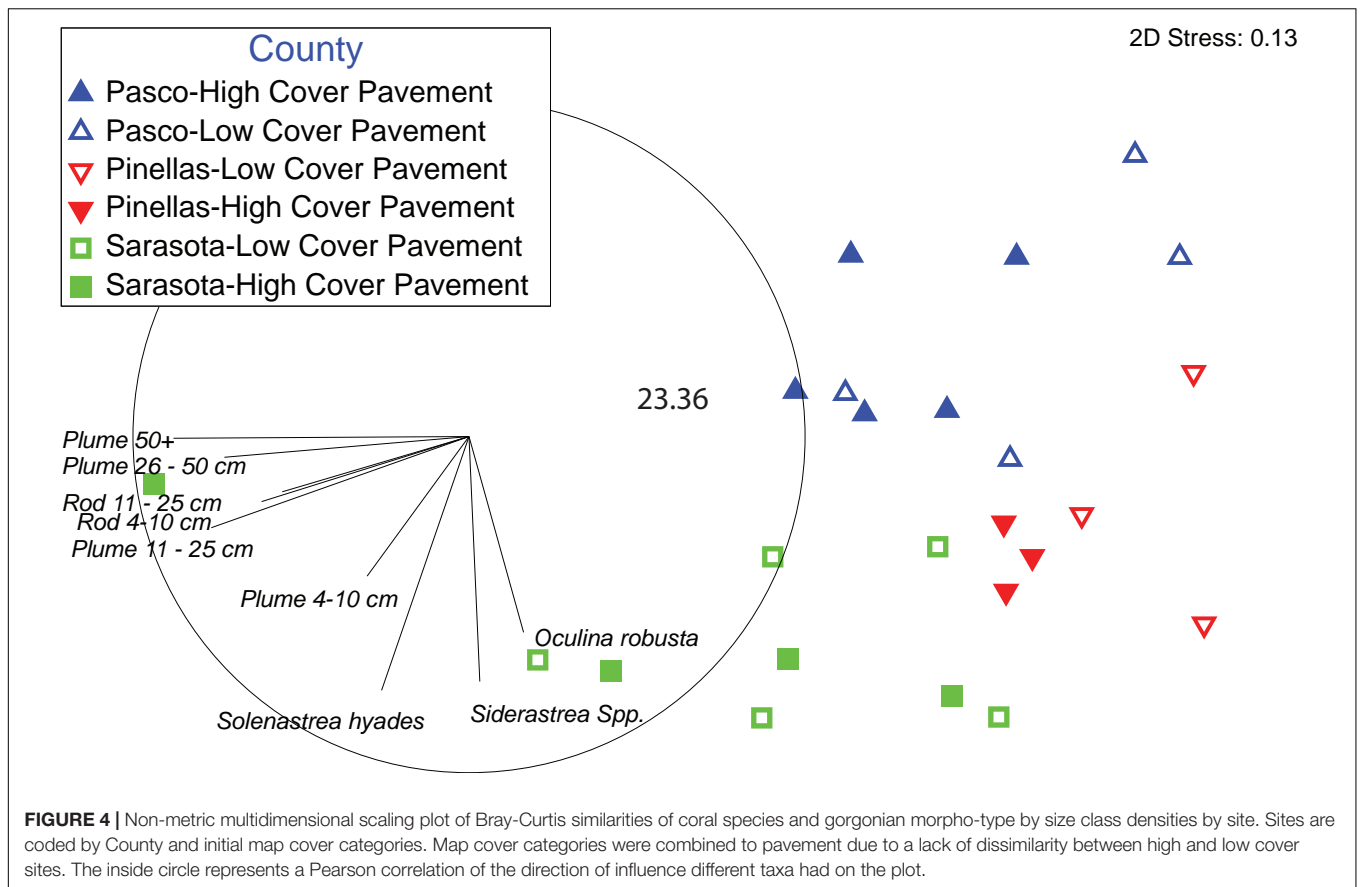
TABLE 4 | Gorgonian morpho-type by size class (cm) with abundance, percent and density.

County	Type	Size (cm)	Pasco		Pinellas		Sarasota	
			Total Abundance	Density (per m ²)	Total abundance	Density (per m ²)	Total abundance	Density (per m ²)
Rod		4–10	16	0.12	0	0	115	0.85
		11–25	90	0.67	4	0.04	425	3.15
		26–50	129	0.96	5	0.07	303	2.24
		50+	21	0.16	0	0	180	1.33
Plume		4–10	0	0.00	0	0	164	1.21
		11–25	0	0.00	0	0	81	0.60
		26–50	1	0.01	1	0.01	199	1.47
		50+	13	0.10	0	0	170	1.26
Fan		4–10	0	0	0	0	0	0
		11–25	0	0	0	0	0	0
		26–50	1	0.01	0	0	0	0
		50+	0	0	0	0	0	0
		Pooled total	271	2.01	10.00	0.13	1,637.00	12.13
Total			1,918	5.43				

County differences in percent cover were most pronounced in Hardbottom with sand veneer, Brown Algae, and *So. hyades*. Mean Hardbottom with a sand veneer cover was significantly higher (ANOVA, $p = 0.03$) in Pasco County ($45.77\% \pm 6.22$ SE) than Sarasota County ($20.65\% \pm 9.67$ SE). Brown algae cover was significantly higher (ANOVA, $p = 0.003$) in Pasco ($11.03\% \pm 2.35$ SE) and Pinellas ($10.88\% \pm 10.65$ SE) than in Sarasota County ($2.25\% \pm 0.62$ SE). *So. hyades* cover was significantly lower (ANOVA, $p = 0.005$) in Pasco County ($0.08\% \pm 0.04$ SE) than Sarasota County ($1.13\% \pm 0.30$ SE).

DISCUSSION

Analyses of shallow-water (< 20 m) habitat mapping and benthic community data near the mouth of Tampa Bay indicate a significant shift in marine benthic communities along the WFS. This change is marked by significant pole-ward decreases in stony coral density and gorgonian density and cover. The habitat mapping showed clear differences in habitat type and coverage between regions with more mapped pavement area in the northern region, however, the percent cover data indicated

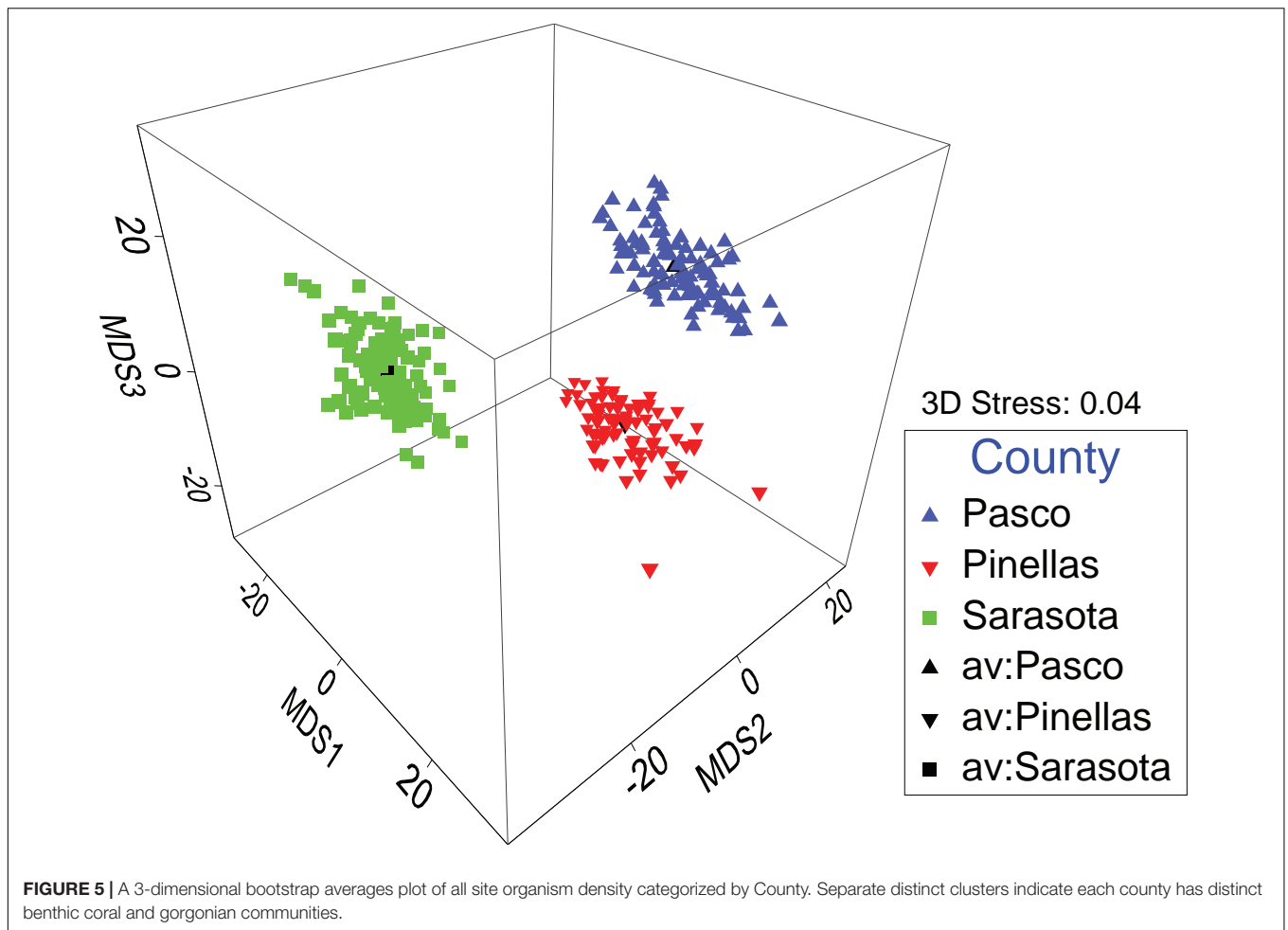


much of this was Hardbottom veneered with sediment. Although there was less pavement in the south, the southern sites had less hardbottom veneered with sediment, and higher coral and gorgonian density and cover. The gap in our mapping and assessments across the mouth of Tampa Bay precluded the ability to specifically identify where these changes occur. Ecoregion boundaries usually vary by the species or the habitat being investigated, and the boundaries do not always change suddenly over a short distance (Engle and Summers, 2000; Toonen et al., 2016). Some may have a broader transition where mobile and short-lived species can vary with seasons as temperature is often a lead determinant of species distributions (Topp and Hoff, 1972; Engle and Summers, 2000; Toonen et al., 2016). As global and local stressors become more prominent, this variability will add to the fuzziness of species boundaries (Briones, 2004; Spalding et al., 2007; Makowski and Keyes, 2011). Thus, this entire area may be part of a larger ecological transition zone (Figure 8). Completing the mapping and conducting assessments in this gap will help identify the best transition location.

Temperature is one of the most important factors affecting WFS coral distributions and ranges as well as a limiting factor for gorgonian and algal cover (Hedgpeth, 1954; Engle and Summers, 1999; Colella et al., 2008; Anderson, 2009; Hale, 2010; Mallinson et al., 2014; Jaap, 2015; Locker et al., 2016; Klaus et al., 2017). The southern WFS is warmer and subjected

to less seasonal variability (Engle and Summers, 2000) and studies around Tampa Bay show distinct changes in water movement that latitudinally affect water temperatures (Hine and Locker, 2011; Jaap, 2015; Weisberg et al., 2016). Smith (1954) identified the 21°C isotherm in January, located at the Pinellas County line just north of Tampa Bay as stated by Fuglister's (1947) atlas of oceanic temperatures, to be the northern limit of coral reefs in the Gulf (Glynn, 1973). The minimum average monthly sea surface temperatures show tight isotherms changing from 20.5 to 18.3°C between Tampa Bay to Hernando Beach. Work (1969) described this area Anclote Key to Aucilla River (north of the 21°C isotherm) as an "extraordinary faunal area" due to the "paradoxically richer number of both Carolinian and West Indian species." *Cladocora*, *Manicina*, *Isophyllia*, *Scolymia*, *Siderastrea*, and *Oculina* corals are common throughout the area (Work, 1969). With the exception of *Isophyllia* and *Scolymia*, his description matches our results throughout our mapped area, indicating that perhaps this extraordinary fauna extends further south than previously realized.

Interestingly, the location of Fuglister's (1947) tight minimum isotherms on the WFS is also where the BFZ crosses north Tampa Bay (Figure 8) (Klitgord et al., 1984). The BFZ is an important feature in the Gulf of Mexico that extends northwest to southeast beneath central peninsular Florida separating Florida's basement rocks (Hine et al., 2008). This zone creates coastal



morphologies that influence ecological changes (Klitgord et al., 1984; Walker, 2012; Walker and Gilliam, 2013). On Florida's East coast, the BFZ is associated with significant changes in benthic and reef fish communities and benthic habitat extent and type (Walker, 2012; Walker and Gilliam, 2013; Fisco, 2016; Ames, 2017). This is the northern range of many sub-tropical flora and fauna on the east coast. To the north of this feature, the shelf expands west and allows the Florida Current to meander creating periodic cold-water upwelling (Walker and Gilliam, 2013), which limits sub-tropical biota. There are significant reef fish and hardbottom community differences north and south of this area (Briggs, 1974; Engle and Summers, 1999; Walker, 2012; Klug, 2015; Fisco, 2016; Ames, 2017) and it separates the EMAP-E West Indian and Carolinian provinces. Thus, it is likely not just a coincidence that the BFZ is a major community transition point on the WFS.

Our results support the Marine Ecoregions of the World and the EMAP-E WFS biogeographic province that illustrate a transition just north of Tampa Bay, FL at Indian Rocks Beach (Hutchins, 1947; Ekman, 1953; Hall, 1964; Gosner, 1971; Briggs, 1974; Spalding et al., 2007). The spatial limits of our work did not allow us to identify the specific biogeographic province transition location between Pinellas and Sarasota or evaluate

other ecoregions south at Cape Romano or north at Cedar Key (Engle and Summers, 2000; Toonen et al., 2016). However, our study spanned an ecoregion boundary at Anclote Key where the benthic communities are dissimilar between Pinellas and Pasco counties. This is not surprising given the tighter isotherms of minimum temperatures north of Tampa Bay (Fuglister, 1947).

Similar to Florida's east coast, there are likely other benthic and reef fish ecoregions along the WFS. Coomans (1962) suggested that WFS faunal breaks occur based on annual surface isotherms of 25°. Previously proposed faunal boundaries of flatfishes include Apalachicola, Cedar Key, Anclote Key, Tampa Bay, Charlotte Harbor, Cape Romano, or Cape Sable (Topp and Hoff, 1972). West Florida shelf flatfish distributions were arbitrarily separated at Tampa Bay because the transition between areas is gradual with some species occurring irregularly and seasonally (Topp and Hoff, 1972). Hedgpeth (1954) and Briggs (1958) identified the southern WFS as one of the four major bottom communities of the Gulf called, "sponge grounds." Fifty-three scleractinian species have been found in this area (Phillips et al., 1990), however, apart from the very southern extent, conditions on the WFS are unfavorable for coral reef development (Jaap, 2015). Most of the West Florida shelf supports low diversity of mostly warm-temperate ahermatypic

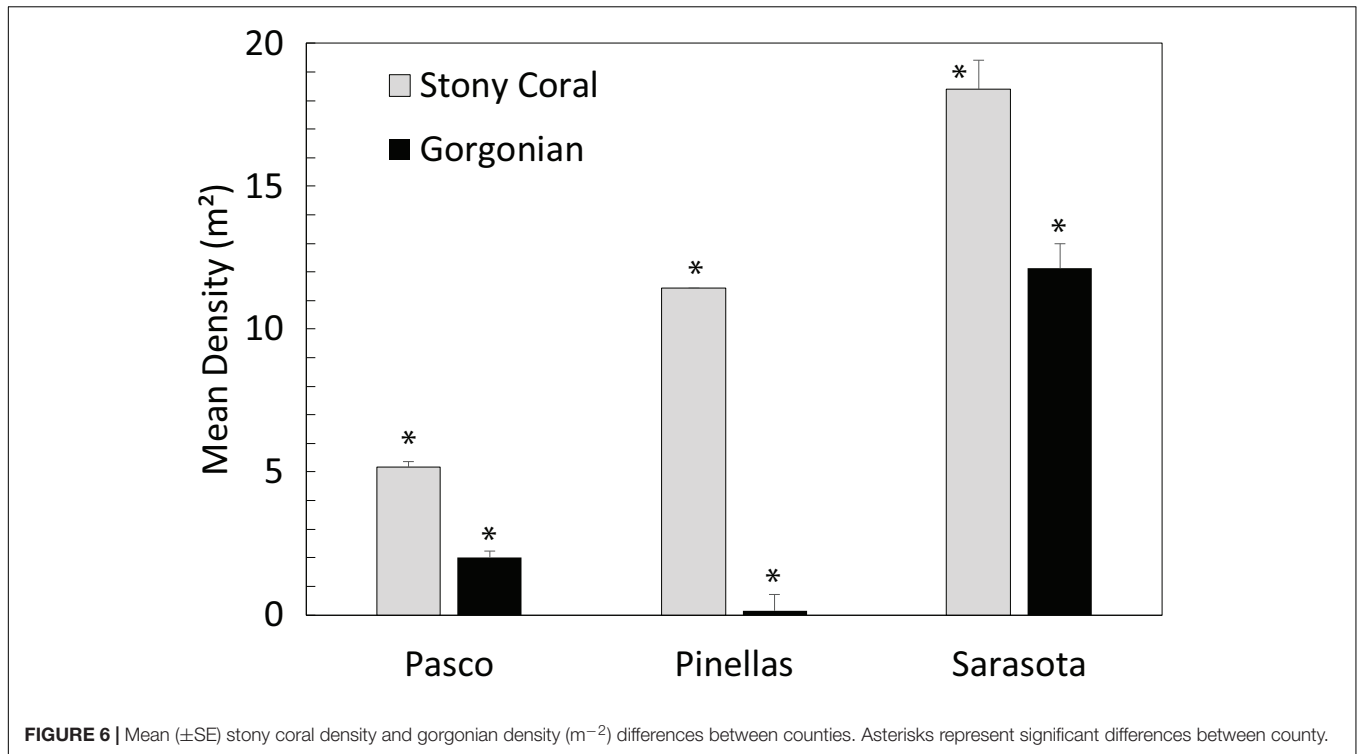


FIGURE 6 | Mean (\pm SE) stony coral density and gorgonian density (m⁻²) differences between counties. Asterisks represent significant differences between county.

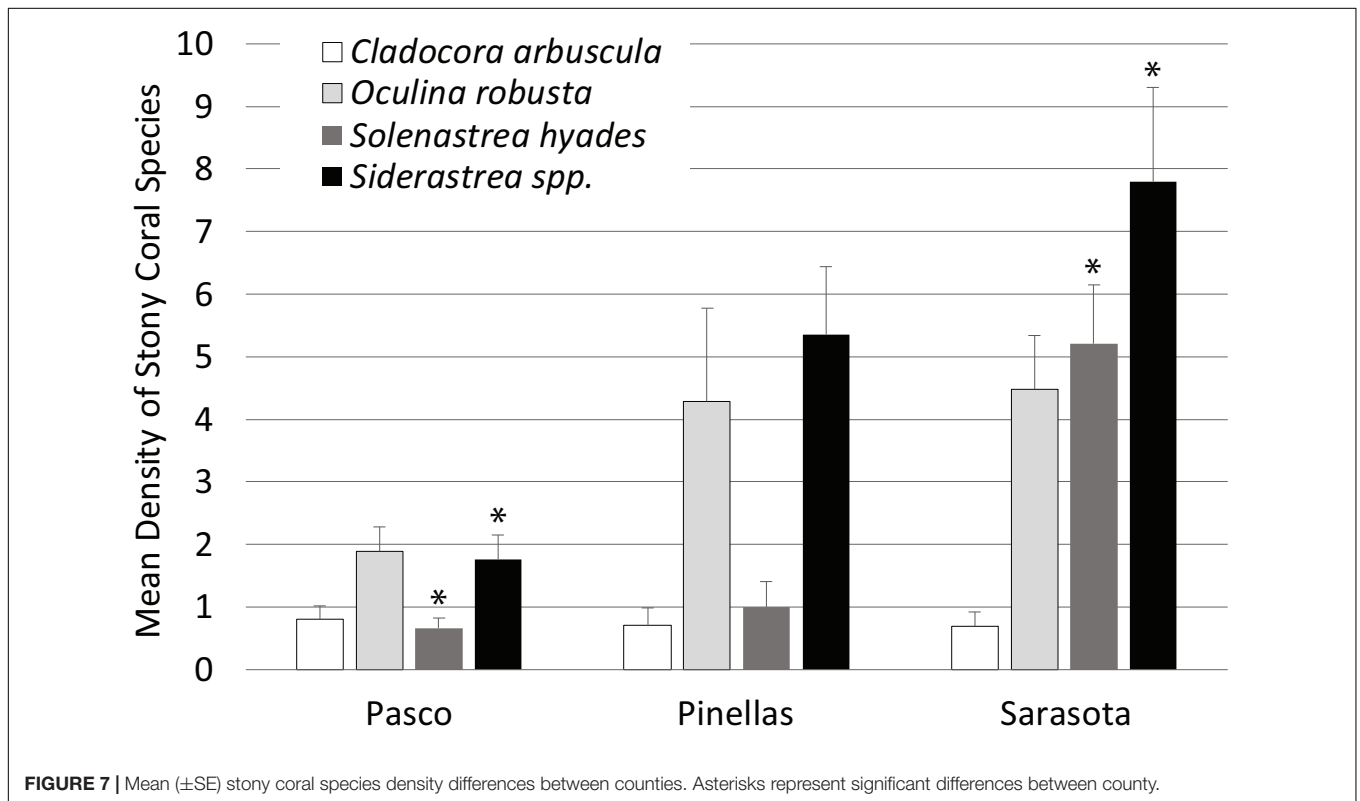


FIGURE 7 | Mean (\pm SE) stony coral species density differences between counties. Asterisks represent significant differences between county.

eurytopic taxa (Jaap, 1984, 2015; Phillips et al., 1990; Lirman, 2013). There is a loss in species richness and major differences in stony coral demographics from southern to northern latitudes

(Jaap, 2015; this study). Ten stony coral species were documented in this study with four dominant species that are tolerant of cold-water temperatures: *Siderastrea* spp., *O. robusta*, *Cl.*

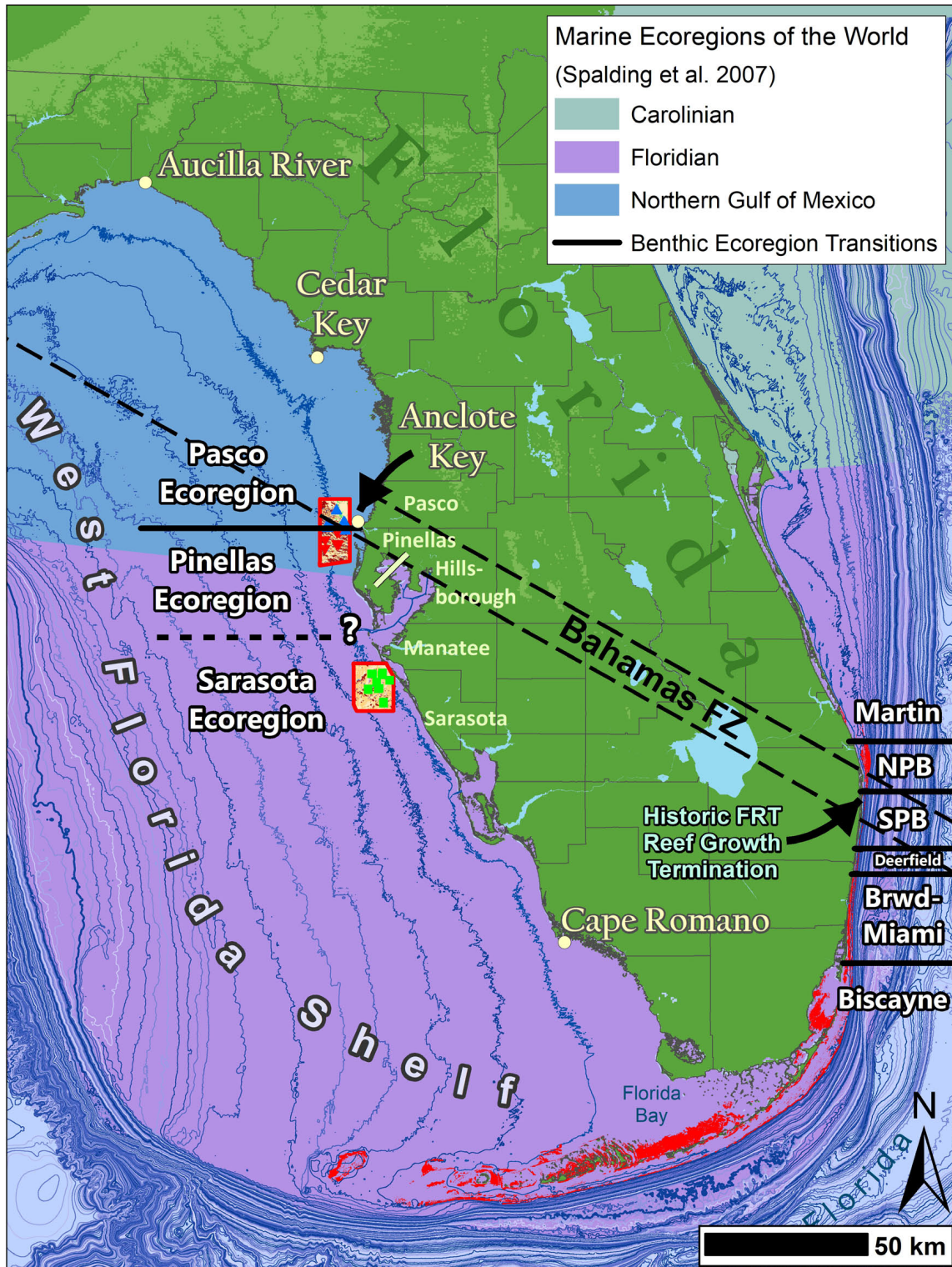


FIGURE 8 | A map of Florida coastal benthic ecoregions overlaying the Marine Ecoregions of the World (Spalding et al., 2007) and the approximate location of the Bahamas Fracture Zone (BFZ) taken from Klitgord et al. (1984). The east coast illustrates the regions from Walker and Gilliam (2013). The west coast are results from this study. There are benthic community shifts along both coasts at the BFZ. On the west coast there is one near the Pinellas and Pasco Countyline and a more pronounced one somewhere between Pinellas and Sarasota counties near Tampa Bay.

arbuscula, and *So. hyades* (Jaap, 1984; Phillips et al., 1990; Lirman, 2013).

Alcyonarian fauna also changes significantly along the west Florida shelf. *Antillogorgia acerosa*, *A. americana*, and *Pterogorgia anceps* are part of a decimated West Indian assemblage that occurs some distance up the west coast of Florida (Bayer, 1954). This group is merged with and then replaced by a distinctly temperate fauna dominated with *Leptogorgia virgulata* and *L. setacea* (both of which are referable, Bayer, 1952 to Verrill's genus *Eugorgia*), and *Muricea pendula* (Bayer, 1954). This assemblage matches that of the Carolina coast (Bayer, 1954). The locations of these changes have not been identified, however, our study found distinct differences in gorgonian densities and sizes north and south of Tampa Bay.

Wide temperature variations can cause significant ecological change in the community structure (Lugo-Fernández et al., 2001; Jaap, 2015). Extended periods of warm or cold temperatures are likely to cause hermatypic coral bleaching, a stress response that can lead to mortality. Our observations were made in August in very warm water (>30°C, Rutgers Coastal Ocean Observation Lab). Three sites were not surveyed due to thick green water with zero visibility at depth. We found that 19% of all corals were at least partially bleached, the majority from two species: *O. robusta* (51.8%) and *So. hyades* (17.1%). *Oculina* corals are not obligate zooxanthellate corals so it is unclear how their bleaching effects their physiology, however, they are known to be dominated by *Symbiodinium* type B1 in the northern Gulf of Mexico (Leydet and Hellberg, 2016), which is a clade that usually dominates in temperate environments (Thornhill et al., 2008) and is more thermally sensitive than type B2 (McGinty et al., 2012). *Symbiodinium* type was unknown in our study, however, it is possible that the warm temperatures caused the release of a clade adapted to the normally cooler temperatures.

Although much bleaching was found, we found no disease or evidence of the stony coral tissue loss disease outbreak that was affecting over 60% of the colonies in its wake (Precht et al., 2016; Walton et al., 2018). The dynamics of coral bleaching, colony recovery and colony mortality are not known for the WFS, however, the small colony sizes indicate these colonies do not survive much more than a decade.

Local bay-specific factors (i.e., surface area or anthropogenic factors) can also affect the distribution of benthic communities (Eidens et al., 2015). Jaap (2015) identified discontinuous and patchy scleractinian corals where large estuaries and bays (such as Tampa Bay) influence salinity altering community structure. The WFS is prone to frequent, significant impact from HAB impacting the water quality and light transmission (Colella et al., 2008; Anderson, 2009). However, prior to 2005, there was only one documented case of a benthic mortality event off Pinellas and Sarasota resulting in benthic die-offs but limited stony coral mortality. The recovery process for the benthic fauna from that event is slow and continues today (Smith, 1975; Colella et al., 2008).

In summary, this study mapped a large expanse of hard bottom and identified a major shift in benthic communities around Tampa Bay, FL highlighting the necessity to continue mapping and benthic characterization on the WFS to understand

the extent of the resources and identify other biogeographic or ecoregion boundaries. These areas serve as nursery and foraging grounds for economically and commercially important species (e.g., grouper, gray snapper, and hogfish) (Jaap, 1984; Simon and Mahadevan, 1985; Rice and Hunter, 1992; Thompson et al., 1999; Coleman et al., 2014; Jaap et al., 2014) whose populations are modeled for fisheries management (Saul et al., 2013). A detailed habitat map will facilitate more precise models of reef-associated species (Grüss et al., 2016; Grüss et al., 2017a,b). These findings also illustrate a need for additional research of the Gulf of Mexico benthic habitats to give a more comprehensive understanding of WFS marine habitat and benthic community biogeography in the context of future warming conditions and the potential tropicalization of the northern Gulf of Mexico. Undocumented changes in ecoregions and shift in transition locations may be presently occurring. We suggest unifying all presently available seafloor mapping data into spatial and categorical GIS databases, mapping new areas with high probability of hardbottom resources, and collecting benthic community data over broader scales to expand the biogeographic analyses and refine community biogeographic zonation. This is a necessary precursor to any long-term community monitoring to detect spatial shifts in communities and population modeling.

DATA AVAILABILITY STATEMENT

The mapping data for this study can be found in GRIIDC at the following URL: <https://data.gulfresearchinitiative.org/data/FL.x710.000:0001>.

AUTHOR CONTRIBUTIONS

BW, SK, and RB contributed conception and design of the study. BW and SK organized the database. CA created the map. CA, SE, and BW performed the statistical analysis. SE and BW wrote the first draft of the manuscript and sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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