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coral reef paper

Spatial variation in hard bottom coral communities of the coastal West Florida Shelf

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ABSTRACT.—Hard bottom coral and sponge communities differ along portions of the West Florida Shelf (WFS) in species occurrence, diversity, and/or size. However, the composition and spatial distribution of these communities are not well understood. Community transitions have been proposed in the central portion of the WFS around Tampa Bay, Cedar Key, and as far south as Charlotte Harbor, but supporting data are sparse. Fifteen sites in three regions of Florida were surveyed for species distribution, density, and demographics. Distinct communities were found between St Teresa, Hudson, and Tarpon Springs. Coral and sponge densities were highest off Tarpon Springs followed by St Teresa and lowest off Hudson. Stony corals (*Siderastrea radians*, *Cladocora arbuscula*, and *Phyllangia americana*) and octocoral complexes (*Muricea* spp. and Plexauridae) were the main drivers of differences between the regions. Several species of corals significantly varied in size between the three regions and stony corals in Tarpon Springs were significantly larger in 2021 than in the same region in 2017. Overall, the communities had healthy corals with no disease and minimal bleaching. This research broadens the understanding of WFS hard bottom communities and their spatial distributions through detailed surveys. Additional research on the hard bottom communities of the WFS is necessary to attain a comprehensive understanding of the coastal shelf and support long-term management.

The West Florida Shelf (WFS) spans Florida's Gulf coast, from the northeastern Gulf of Mexico to the Florida Keys. This shelf is characterized by varying seafloor morphologies, sediment types, levels of exposed substrate, and biological communities. The continental shelf and slope of west Florida exist within the Florida Platform, an ancient 900-km long, 1000-km wide, and 12-km thick carbonate platform underlying the entire state and its continental margins. In their broad scale assessment of mapping surveys, Keenan et al. (2022) estimate 2.7% of the eastern GOM shelf is natural hard bottom habitats, yet a fraction of those habitats has been investigated

(Obrochta et al. 2003, Keenan et al. 2022). The structure and exposed substrate of these natural hard bottom habitats are ideal for colonization by sessile organisms.

Benthic communities on the hard bottom habitats of the WFS include algae, stony corals, octocorals, sponges, and tunicates. These organisms create three-dimensional structures that provide habitat for a range of motile organisms, including important fisheries species. In particular, the hard bottoms on the inner WFS provide substrate for the breeding, spawning, and growth of economically valuable commercial and recreational fisheries such as grouper, snapper, and hogfish (Switzer et al. 2020). The diversity, abundance, and biomass of fishes are higher on hard bottom structures with sessile invertebrates than those without, making sessile organisms critical for fisheries stability (Kendall et al. 2009).

The natural hard bottom communities of the WFS are largely unclassified compared to their counterparts in the Florida Keys and on the eastern Florida coast (Hine and Locker 2011, Jaap 2015). Although natural hard bottom habitats comprise a small portion of the WFS seafloor, their associated fauna create structure of critical importance for commercial and recreational fisheries (Keenan et al. 2022). Shelf-edge benthic communities in deeper water, such as Pulley Ridge and the Florida Middle Grounds have been relatively well studied, but most of the WFS hard bottom communities are virtually understudied (Phillips et al. 1990, Mallinson and Coleman 2007, Koenig and Coleman 2008). Hard bottom coral communities are ecologically and economically valuable. The federal government protects these coral habitats as "Essential Fish Habitats" (EFH) under the 1996 Magnuson-Stevens Fishery Management and Conservation Act. The structures created by corals and sponges provide refuge, shelter, and nursery grounds for commercial and recreational fisheries. These habitats are also of importance for tourism, especially in the central and southern portions of the shelf.

The WFS region has been broken into two marine provinces according to the Environmental Monitoring and Assessment Program for Estuaries (EMAP-E). These include the West Indian province, which spans from Jupiter Inlet on the east coast of Florida to Tampa Bay, Florida, and the Louisianan province, which spans from Tampa Bay, Florida to the Texas coast (Engle and Summers 2000). However, a single boundary at Tampa Bay does not describe the communities and species distributions along the shelf. Due to a lack of comprehensive community data, other studies have suggested boundaries both north and south of Tampa Bay (Engle and Summers 2000, Toonen et al. 2016). Most notably, Walker et al. (2020) found evidence of an ecoregion boundary for stony corals at the mouth of Tampa Bay and another near the border of Pasco and Pinellas counties. These findings suggest the existence of smaller ecoregions along the inner WFS that may be correlated with local environmental conditions.

Seawater temperature is one of the known drivers in shaping the spatial distribution of benthic communities (Assis et al. 2017). The inner WFS spans over 6.5° in latitude and crosses through areas of varying environmental conditions. A climate gradient exists along the WFS with the northern extent categorized as warm-temperate and the southern portion as subtropical (Spalding et al. 2007). During the peak of the cold season, sea surface temperatures reach below 18 °C from the northern shelf to just south of Cedar Key, Florida (Morey et al. 2017). For tropical corals, 18 °C is generally considered to be the minimum threshold temperature (Kleypas et al. 1999). Corals inhabiting the northern shelf region must be adapted for colder peak temperatures than further south where peak cold temperatures range between 18 and 21 °C (Morey et al. 2017). This climate gradient has been linked to latitudinal variations in fish communities as well as benthic macroinvertebrates, algae, and others (Engle and Summers 2000, Canning-Clode 2009, Walker and Gilliam 2013, Toonen et al. 2016). Other factors including hydrodynamics, harmful algal blooms (HABs), rivers, and other local influences may contribute to differing coral and sponge communities along the WFS.

Due to the large latitudinal extent (24.5°N to 30°N) of the shelf, as well as results from previous studies (Walker et al. 2020), there is reason to believe the composition of hard bottom communities will shift along the length of the inner shelf. The goal of this study was to survey hard bottom sites in the north and central portions of the WFS in order to identify differences in benthic community composition and pinpoint where these differences occur. Data on the range and distribution of critical species will allow conservation and management plans to be tailored to better identify areas for protection as well as to manage fishing and destructive practices across vital portions of the shelf. With information on hard bottom community structure and distributions, state agencies will be better able to create specialized conservation and fisheries management plans to improve ecosystem monitoring and management of economically valuable fisheries.

Materials and Methods

Study Sites.—Three regions of the west Florida coast were used for this study: a northern region offshore of St Teresa (Franklin County), a central region offshore of Hudson (Pasco County), and a southcentral region offshore of Tarpon Springs (Pasco County; Fig. 1). A combination of existing bathymetric maps, satellite, and sonar data was used to identify hard bottom areas of similar relief in 10–20 m depth (Baumstark et al. 2016), from which five sites were selected for survey within each region.

Community Data.—Study sites were surveyed in August 2020 (St Teresa), February 2021 (Tarpon Springs), and June 2021 (Hudson) by SCUBA divers, who utilized modified methods from Walker et al. (2020) for community composition data collection. Four non-overlapping, parallel 30 m transects were set at each site. Parallel transects allowed for ample coverage of the hard bottom ledges without surveying overlapping areas or the transects running off the ledge. A GoPro camera was mounted to a square PVC quadrat (0.5 × 0.5 m) and used to take downward facing video, pausing every 0.5 m along each transect. From the videos, stony corals and octocorals were identified to the highest taxonomic resolution possible and counted to obtain density measurements. Sponges were classified into 11 different functional growth forms as outlined by Schönberg et al. (2014) and counted for density measurements. Additional photos and/or videos were taken to help with species identification. Collections were taken of unknown individuals whose identification could not be resolved from images.

Percent cover of overall benthic organisms was estimated from 60 random quadrat photographs at each site using Coral Point Count with excel extensions (CPCe; Kohler and Gill 2006). Twenty random points were assigned to each image and the bottom cover was classified into two categories, presence or absence of target organisms (stony corals, octocorals, and sponges). Due to their height and flexible

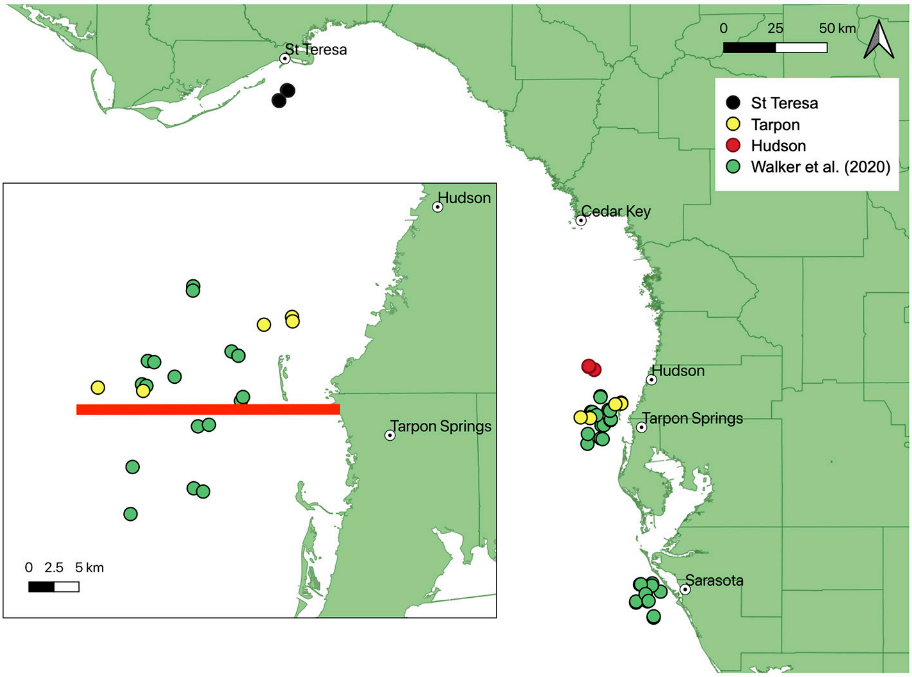

Figure 1. Map of study area. Sites (yellow circles) and proposed ecoregion boundary (red line) from Walker et al. (2020) are included.

structure, octocoral colonies can extend past the bounds of the camera quadrat. Therefore, higher resolution taxonomic classification was not possible due to the potential for underrepresentation of the coverage of octocorals.

Statistical analyses were done in PRIMER v6 (Clarke and Gorley 2005) as it is designed for complex community data that do not fit the requirements of parametric statistics, as they generally are not normally distributed with homoscedastic variance. The overall community and percent cover data were transformed using a square root transformation to reduce the relative influence of common species. Nonmetric multidimensional scaling (NMDS) plots with clustering were created using Bray–Curtis dissimilarity indices. One-way analysis of similarity (ANOSIM) using Bray–Curtis matrices was used to determine whether there were differences in community structure and percent cover between regions. Bray–Curtis distance was used due to the presence of zeros in the dataset (denoting an absence of a species/group) to ensure that the absence of species did not influence region similarity. A similarity percentage analysis (SIMPER) was performed to determine the species most responsible for observed differences between the regions. In addition, a one-way analysis of variance (ANOVA) was used to determine whether there was an effect of region on mean density by taxa.

Community data for three additional regions from Walker et al. (2020) were included to test for larger-scale community trends across a total of six regions. A separate one-way ANOSIM for community composition was done using factors consistent with Walker et al. (2020). For consistency between the datasets, only stony corals larger than 4 cm were included in the analysis and the octocoral categories were modified from species to size class and morphological bins (rod, plume, fan). Sponge groups were not included in this analysis.

Stony Coral Health Data.—From the community data transect videos, stony coral colonies showing signs of bleaching were noted and tallied by species into three categories: paling, partially bleached, or fully bleached. Stony coral colonies were also observed for signs of disease. Due to the low prevalence of bleaching, all signs of bleaching were combined for analysis as a percentage of the total number of colonies per site. A one-way ANOSIM using Euclidean matrices was used to determine whether there were differences in the percentages of colonies with signs of bleaching between regions. Euclidean matrices were used to reflect metric distances, in that sites with zeros (absence of bleaching) will be similar.

Coral Size Data.—At each site, two transects were surveyed for a total of 30 m^2 to gather data on coral demographics. Stony corals and octocorals greater than 4 cm were identified and measured in situ for max length, height, and width to the nearest centimeter. Additional size data were obtained from surveys done in 2017 to test for temporal changes in stony coral size in Pasco County (Eagan 2019, Walker et al. 2020). The size data were analyzed in SigmaPlot v13.0 (Systat Software Inc.). A one-way ANOVA was used to determine whether there was an effect of region on mean coral size by taxa. The Holm–Sidak method was used for post-hoc pairwise multiple comparisons between regions, with reports on the difference of means (DM). For the size data, each species or complex was analyzed individually, using methods most suitable for the species-specific growth pattern. The stony corals *Cladocora arbuscula, Siderastrea radians,* and *Manicina areolata* were analyzed using area measurements ($\pi \times r_1 \times r_2$) due to their outward, rather than vertical, growth pattern. The stony corals *Oculina* spp., *Solenastrea hyades*, and all octocorals were analyzed using height values due to their principally vertical growth.

Environmental Data.—Chlorophyll-*a* (Chl-*a*) values were collected from the NOAA NESDIS CoastWatch database from the VIIRS instrument on the S-NPP satellite using a blue-green reflectance ratio. Seasonal concentrations were created from averages of daily mean grids, from 2012 to 2020, at approximately 840-m resolution. Values for each region were taken from the closest data point to the geographic mean of the sites in the region. Seasonal Chl-*a* values were averaged over their respective timespans to produce a single value for the region.

Results

Community Composition.—A total of 15 sites were surveyed for a total area of 900 m^2. In total, 11,448 stony corals, 3218 octocorals, and 8692 sponges were identified and counted for use in community analysis. A one-way ANOVA showed that the three regions varied significantly in density of total stony corals ($F_{2,12} = 11.07$, $P = 0.002$) and sponges ($F_{2,12} = 12.20$, $P < 0.001$; Fig. 2). Holm–Sidak post-hoc testing identified that the Hudson region had significantly lower densities of stony corals than both Tarpon (DM = 15.50, $t = 4.70$, $P = 0.002$) and St Teresa (DM = 7.21, $t = 2.18$, $P = 0.049$). The Hudson region also had significantly lower densities of sponges compared to Tarpon (DM = 8.51, $t = 4.93$, $P = 0.001$) and St Teresa (DM = 4.66, $t = 2.70$,

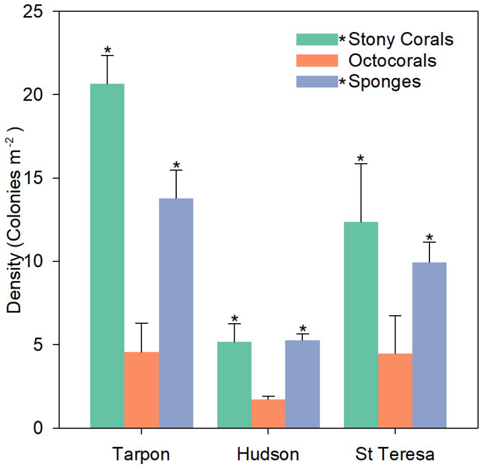

Figure 2. Overall density of stony corals, octocorals, and sponges by region. Density values are in individuals per m^2 and include values from all sites within a region. Error bars reflect standard error of the mean, and asterisks indicate significant differences between regions.

$P = 0.038$). Though the density of octocorals did not vary greatly between regions (alpha = 0.05), the compositions did. ANOSIM found no significant differences in the percent cover of target organisms between regions ($P > 0.05$).

Of the stony corals, *S. radians* was the most common with 5881 individual colonies, followed by *C. arbuscula* with 3464 colonies. Other widespread stony corals included *S. hyades*, *M. areolata*, and *Oculina* spp. Several stony coral species were very rare (<0.4% of all colonies) including *Montastraea cavernosa*, *Porites divaricata*, *Stephanocoenia intersepta*, *Scolymia* sp., and the fire coral *Millepora complanata*. One cup coral species, *Phyllangia americana*, was found in high abundance with 706 individuals, but a significant majority (99.7%) of all colonies were found in the St Teresa region ($F_{2,12} = 16.24$, $P < 0.001$).

Within each region, *S. radians* was the dominant stony coral followed by *C. arbuscula*, comprising at minimum 69.0% of all stony coral colonies found within a region (Fig. 3). The mean densities of these two corals varied significantly between regions (*S. radians:* $F_{2,12} = 26.99$, $P < 0.001$; *C. arbuscula:* $F_{2,12} = 8.27$, $P = 0.006$). The third-most dominant coral varied by region including *S. hyades* in Tarpon, *Oculina* spp. in Hudson, and the cup coral *P. americana* in St Teresa.

Of the octocorals, two groups were most common over the study area, Plexauridae and *Muricea* spp., that comprised 87.4% of all octocorals classified (Fig. 4). In the Tarpon and Hudson regions, octocorals of the Plexauridae were most common, while in St Teresa, *Muricea* spp. was most common. Other octocorals in the study area included *Leptogorgia virgulata, Leptogorgia hebes, Pterogorgia anceps, Carijoa riisei,* and *Antillogorgia acerosa*. Though densities of total octocorals were significantly similar across the study area, densities of *L. virgulata* and *C. riisei* significantly varied between the three regions (*L. virgulata:* $F_{2,12} = 15.06$, $P < 0.001$; *C. riisei:* $F_{2,12} = 8.96$, $P = 0.004$). *Leptogorgia virgulata* was found more commonly in St Teresa than the other two regions, and *C. riisei* was only found in St Teresa.

Sponges were classified into 11 different functional growth groups as described by Schönberg et al. (2014) as in situ identification without spicule analysis is impractical

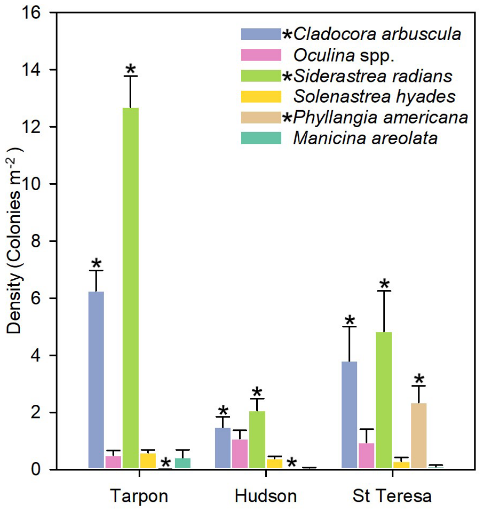

Figure 3. Most abundant stony corals by region. Dominance of corals are shown via density measurements of individuals per m^2. All transects and sites within a region are averaged to show regional density values. Error bars reflect standard error of the mean, and asterisks indicate significant differences between regions.

for most species. Of these, three groups contained encrusting forms: encrusting-creeping (EN-cg = creeping, ramose), encrusting-endolithic (EN-en = endolithic, bioeroding), and encrusting forms (EN-cr). Three groups contained massive growth forms: massive-simple (M-s = simple; large, lumpy sponges with inhalants and exhalants scattered on surface), massive-ball (M-bl = spherical sponges), and massive-cryptic (M-crp = cryptic sponges, embedded in sediment with elevated fistules or cone-shaped portions). Four groups were cup-like growth forms: cup-incomplete

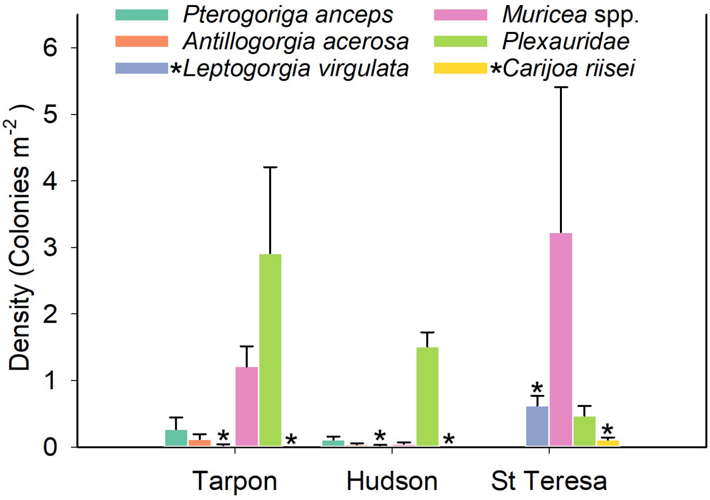

Figure 4. All octocorals by region. Dominance of octocorals is shown via density measurements of individuals per m^2. All sites within a region are averaged to show regional density values. Error bars reflect standard error of the mean, and asterisks indicate significant differences between regions.

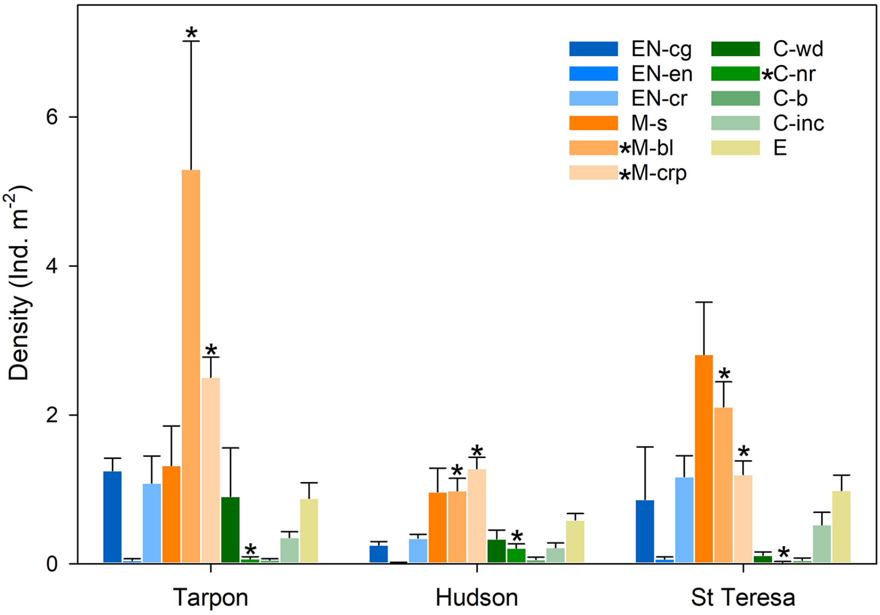

Figure 5. All sponge groups by region. Dominance of sponge groups are shown via density measurements of individuals per m^2. All sites within a region are averaged to shown regional density values. Encrusting groups are shown in varying shades of blue, massive groups in orange, cup-like groups in green, and erect groups in yellow. Error bars reflect standard error of the mean, and asterisks indicate significant differences between regions.

(C-inc = incomplete cup, curled fan), cup-wide (C-wd = wide cup or goblet), cup-barrel (C-b), and cup-narrow (C-nr = narrow cup or tube). The final group contained erect sponges (E).

Massive sponges were the most common overall (Fig. 5). Of these, M-bl sponges were most dominant at 29.0% of all sponges classified, with significantly higher densities found in Tarpon ($F_{2,12}$ = 4.84, P = 0.029). Tarpon also had higher densities of M-crp sponges than the other two regions ($F_{2,12}$ = 12.38, P = 0.001), while Hudson had the highest density of C-nr ($F_{2,12}$ = 7.34, P = 0.008). All of the 11 morphotypes were found in each of the three regions.

Results of the SIMPER analysis for each region are described below; these show the mean densities of major taxa, average site similarity, and taxa contributing most to site similarity.

Tarpon Region.—Stony corals (20.65 m^{-2}) and sponges (13.78 m^{-2}) contributed most to overall density, and each contributed approximately 41.2% to the overall community similarity. Sites had an average similarity of 77.5%. Eight taxa contributed to 72.0% of the community similarities. The five taxa with the greatest densities were two stony coral species, *S. radians* (12.68 m^{-2}) and *C. arbuscula* (6.26 m^{-2}), and three sponge groups, M-bl (5.30 m^{-2}), M-crp (2.51 m^{-2}), and EN-cg (1.25 m^{-2}).

Hudson Region.—Sponges (5.27 m^{-2}) and stony corals (5.15 m^{-2}) contributed most to the overall density. Sponges (47.6%) contributed most to overall community

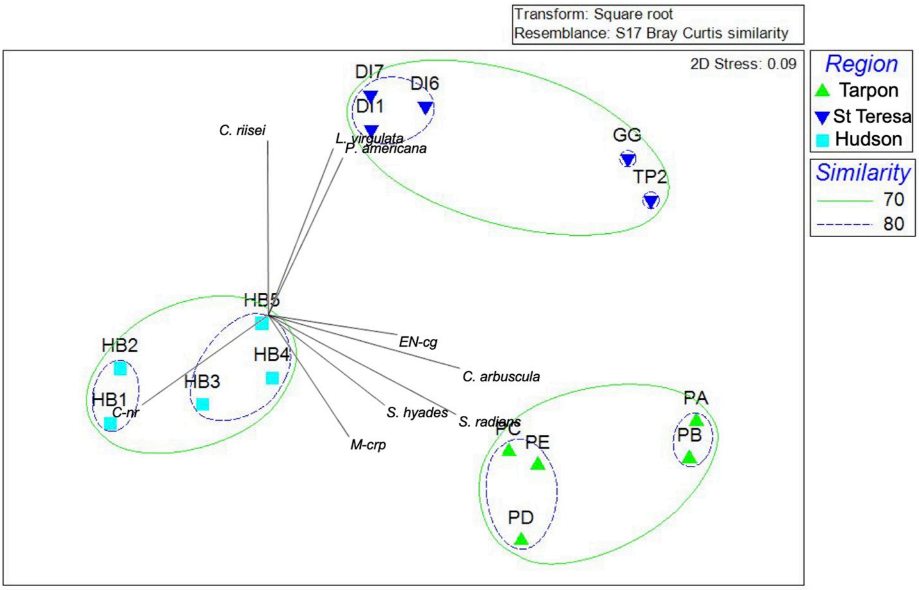

Figure 6. NMDS plot showing the community distributions of sites. Significant clustering by region is observed. Pearson correlation (>0.6) shown as black lines.

similarity, followed by stony corals (33.1%) and octocorals (10.3%). Sites had an average similarity of 80.7%. Nine taxa contributed to 74% of the community similarities. The five taxa with the greatest densities were *S. radians* (2.07 m^{-2}) and *C. arbuscula* (1.48 m^{-2}), octocorals of Plexauridae (1.51 m^{-2}), and the sponge groups M-crp (1.28 m^{-2}) and M-bl (0.98 m^{-2}).

St Teresa Region.—Stony corals (12.36 m^{-2}) and sponges (9.93 m^{-2}) contributed most to the overall density. Sponges (41.3%) contributed most to overall community similarity, followed by stony corals (37.7%) and octocorals (10.9%). Sites had an average similarity of 76.4%. Nine taxa contributed to 74% of the community similarities. The five taxa with the greatest densities were three stony coral species, *S. radians* (4.85 m^{-2}), *C. arbuscula* (3.81 m^{-2}), and *P. americana* (2.35 m^{-2}), and two sponge groups, M-s (2.81 m^{-2}) and M-bl (2.11 m^{-2}).

For community analysis, all transects within a site were averaged for single site values. ANOSIM showed significant differences in distribution by region ($R = 0.94$, $P < 0.001$). Sites in each region clustered together at over 70% similarity, with some within-region clustering particularly in the Tarpon and St Teresa regions (Fig. 6). Depth was not found to influence these within-region groupings ($P > 0.05$). Pairwise tests supported the significant differences between Tarpon and St Teresa ($R = 0.91$, $P < 0.008$), Tarpon and Hudson ($R = 0.99$, $P < 0.008$), and St Teresa and Hudson ($R = 0.92$, $P < 0.008$). ANOSIM on the community data combined with Walker et al. (2020) found no significant difference between any of the six regions, including between the three regions in this study: Tarpon, Hudson, and St Teresa ($P > 0.05$).

SIMPER analyses also determined the main contributors for regional dissimilarly. The Tarpon and St Teresa regions were an average of 34.4% dissimilar. *Siderastrea*

Table 1. Bleaching prevalence of stony coral species by region, as number of individual colonies and percent of total colonies in the region. Colonies with signs of bleaching (SOB) include paling, fully bleached, and partially bleached colonies.

Region (Sampling Month)	*Cladocora arbuscula*	*Oculina* spp.	*Siderastrea radians*	*Solenastrea hyades*	*Phyllangia americana*	*Manicina areolata*
St Teresa (August)						
Total colonies	1,142	286	1,454	87	704	29
Colonies with SOB	39	20	83	6	3	0
Percent	3.4%	7.0%	5.7%	6.9%	0.4%	0.0%
Hudson (June)						
Total colonies	444	323	622	115	0	15
Colonies with SOB	12	32	61	25	0	1
Percent	2.7%	9.9%	9.8%	21.7%	- - -	6.7%
Tarpon (February)						
Total colonies	1,878	151	3,805	177	2	123
Colonies with SOB	24	2	15	4	0	0
Percent	1.3%	1.3%	0.4%	2.3%	0.0%	0.0%
Total						
Total colonies	3,464	760	5,881	379	706	167
Colonies with SOB	75	54	159	35	3	1
Percent	2.2%	7.1%	2.7%	9.2%	0.4%	0.6%

radians was the highest contributor for dissimilarity (11.0%), followed by *P. americana* (10.6%) and Plexauridae (8.2%). The Tarpon and Hudson regions were 35.8% dissimilar; again, *S. radians* was the highest contributor (17.6%), followed by *C. arbuscula* (10.8%) and M-bl (9.6%). Between St Teresa and Hudson, the average dissimilarity was 35.6% with *P. americana* contributing the most (13.3%), followed by *Murcia* spp. (11.1%) and M-s sponges (6.5%). Between Tarpon and St Teresa and St Teresa and Hudson, 11 taxa contributed to 70% of the dissimilarity while between Tarpon and Hudson, 10 species contributed the same amount.

Stony Coral Health.—There were no instances of coral disease observed throughout the study. Out of the 11,357 stony coral colonies observed, only 11 colonies were fully bleached. Partial bleaching or paling was more common, yet still low overall with 327 colonies showing signs of bleaching (<3.0% of total colonies). All signs of bleaching, including fully or partially bleached and paling, were combined for analysis. ANOSIM showed significant differences in the percent of colonies with signs of bleaching between regions ($R = 0.35$, $P < 0.006$). Hudson saw the highest signs of bleaching overall (8.6%), followed by St Teresa (4.1%) and Tarpon (0.7%). Overall, *S. hyades* was the species most commonly observed showing signs of bleaching with 9.2% of the total *S. hyades* colonies affected. *Oculina* spp. was next-most common (7.1%), followed by *S. radians* (2.7%), *C. arbuscula* (2.2%), *M. areolata* (0.6%), and *P. americana* (0.4%; Table 1).

Coral Size Distributions.—A one-way ANOVA showed that mean Plexauridae sizes were significantly different between the three regions ($F_{2,438} = 23.06$, $P < 0.001$). Holm–Sidak post-hoc testing showed that Plexauridae heights were significantly larger in Hudson than in St Teresa (DM = 16.36, $t = 6.36$, $P < 0.001$) and Tarpon (DM = 7.80, $t = 4.41$, $P < 0.001$).

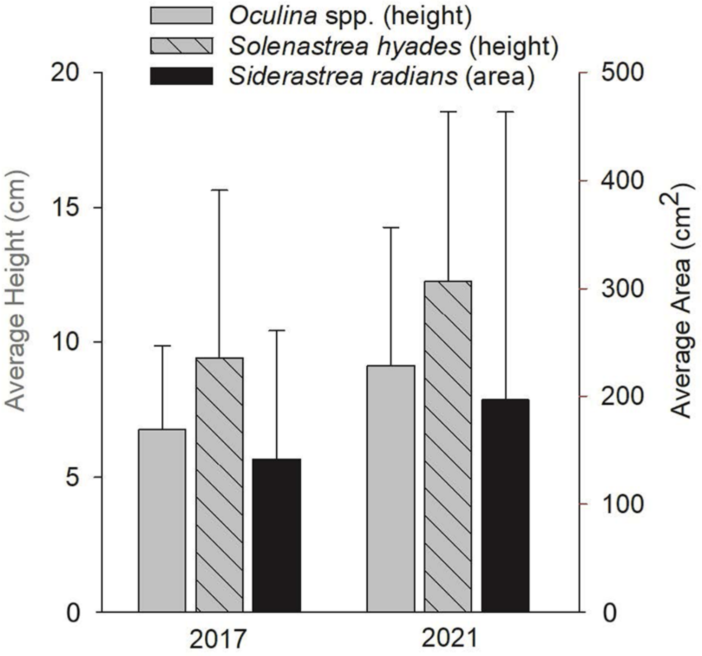

Figure 7. Average sizes of stony corals in the Pasco County area from 2017 and 2021. *Oculina* spp. and *Solenastrea hyades* (grey) height values are shown, while *Siderastrea radians* (black) is shown as area. Error bars show standard deviation from the mean.

The Tarpon region was surveyed in March of 2021 and overlaps an area in the Pasco region that was surveyed by Walker in July of 2017. Four species of stony coral were compared between the 2017 and 2021 datasets: *Oculina* spp., *S. hyades, S. radians*, and *C. arbuscula.* A one-way ANOVA found that Tarpon corals were significantly larger in 2021 than 2017 for three species, *Oculina* spp. ($F_{1,289} = 14.89$, $P < 0.001$), *S. hyades* ($F_{1,138} = 14.89$, $P = 0.01$), and *S. radians* ($F_{1,427} = 8.01$, $P = 0.005$; Fig. 7). There was no significant difference for *C. arbuscula* ($P > 0.05$).

Discussion

Analyses of the shallow-water hard bottom communities north of Tampa Bay indicate significant spatial differences in the benthic communities. These differences are denoted by decreases in stony coral, octocoral, and sponge densities, moving north from Tarpon to Hudson as well as moving south from St Teresa to Hudson. Tarpon had the highest densities of stony corals, octocorals, and sponges, while Hudson, less than 25 km away, had the lowest. The mechanism driving the community differences is still unknown. The proximity of the Tarpon and Hudson regions can point to the existence of an ecoregion boundary with distinct communities (Engle and Summers 2000). Ecoregion boundaries can be species-specific and vary seasonally. Additional surveys between the Tarpon and Hudson regions are needed to pinpoint if and where a boundary or transition zone occurs (Fig. 8).

One possibility for the significantly different communities in this area is water movement around Tampa Bay that influences temperature, harmful algal blooms,

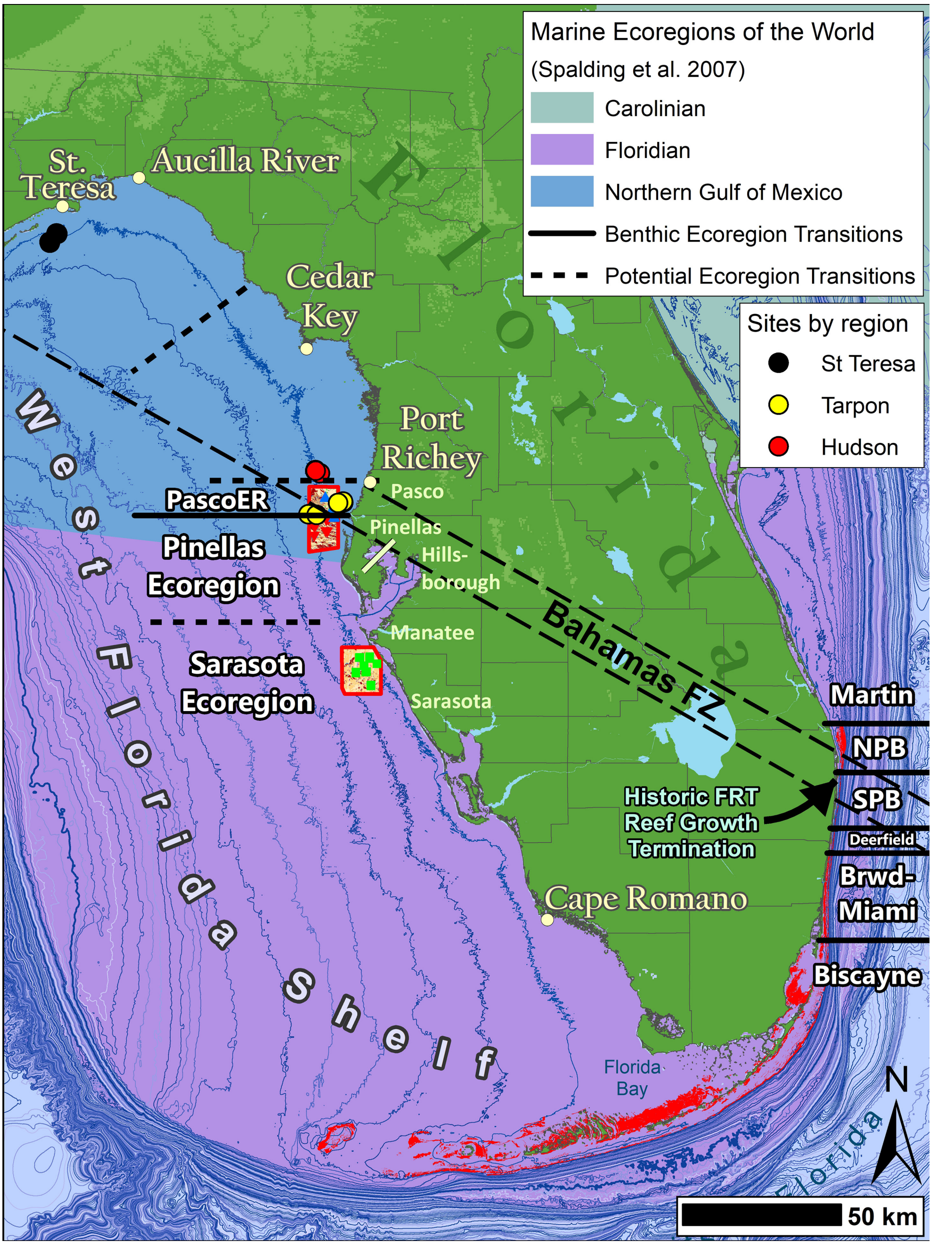

Figure 8. A map of Florida coastal benthic ecoregions adapted from Walker et al. (2020) updated with recent study sites by region. Lines extending from the shelf represent ecoregion or potential ecoregion transitions for the nearshore areas. The Bahamas Fracture Zone (FZ) is represented by the diagonal dotted lines through the shelf. This study identified additional potential ecoregion boundaries near Port Richey north of Tampa Bay and somewhere between Port Richey and St. Teresa to the north.

nutrients, and/or coral larval recruitment. Studies have noted the existence of a zone, beginning just north of Tampa Bay and extending south to the Florida Keys, where there is little surface mixing with deeper, offshore waters (Yang et al. 1999, Klaus et al. 2017). In this zone, termed the forbidden zone, subsurface waters can still be advected to the shoreline of Tampa Bay through bottom transport, as is seen in *Karenia brevis* bloom generation (Weisberg et al. 2019). However, variation in the upwelling strength on the WFS, gyres, and tropical storms can restrict this transport pathway to the shoreline on variable time scales (Weisberg and He 2003, Weisberg et al. 2014). These anomalous events can restrict offshore water flow to nearshore communities and alter the nutrients, temperature, larval recruitment and *K. brevis* bloom strength of the nearshore region. Due to anomalous flow events, benthic communities in this region can see highly variable environmental and nutrient conditions on various time scales which can contribute to differences in coral communities.

The Bahamas Fracture Zone (BFZ) cuts through the Pasco County region and is another possible influence on the Tarpon and Hudson communities. Two community shifts have been proposed for stony corals by Walker et al. (2020), one just south of this study area at the Pasco/Pinellas border and another between Pinellas and Sarasota counties. The authors suggest the coastal morphologies due to the presence of the BFZ have an influence on the communities on either side of the Pasco/Pinellas border. On the east coast of Florida, the BFZ has been linked to differences in benthic habitat type and communities (Walker 2012). Due to the width of the BFZ, that runs diagonally across the state of Florida, its influence on the coastal morphology likely extends past the transition zones proposed by Walker et al. (2020) and can be an influence on the community trends in the north-central portion of the WFS.

The hardbottom communities of St Teresa varied significantly from the other two regions. Though the geographical gap in surveys between the St Teresa and Hudson regions preclude the ability to identify whether there are distinct ecoregion boundaries or a transition zone, the communities are significantly dissimilar. The St Teresa region off the Florida Panhandle shows a greater density of stony corals, octocorals, and sponges than the Hudson region, even with generally colder temperatures year-round (Morey et al. 2017). Temperature can affect metabolism, symbioses, calcification rates, disease susceptibility, oxygen levels, and other critical dynamics for benthic organisms (Clausen and Roth 1975, Peck 2005, Ruiz-Moreno et al. 2012). For tropical species, higher seawater temperatures and solar irradiation are linked to high species diversity and faster growth (Hoeksema 2007). On the WFS, the southern regions (Hudson and Tarpon) are warmer and experience less seasonal variability in temperature, which potentially creates more suitable conditions for coral growth (Engle and Summers 2000). However, the higher density of organisms in St Teresa than in Hudson partially contradicts this idea. A combination of local and regional factors may contribute to this ecological variability. Local influences can be inconsistent and therefore difficult to measure but may play an important role in the composition of hard bottom communities. On a smaller scale, within-region clustering was observed between sites in the Tarpon and St Teresa regions and not attributed to depth. It is likely that local factors also influence the grouping of sites within a region.

One factor in particular that may be structuring the hard bottoms in the St Teresa region is its proximity to the Apalachicola River. The Apalachicola River has been shown to have seasonal cycles in its flow rate and variability, with peaks in the late

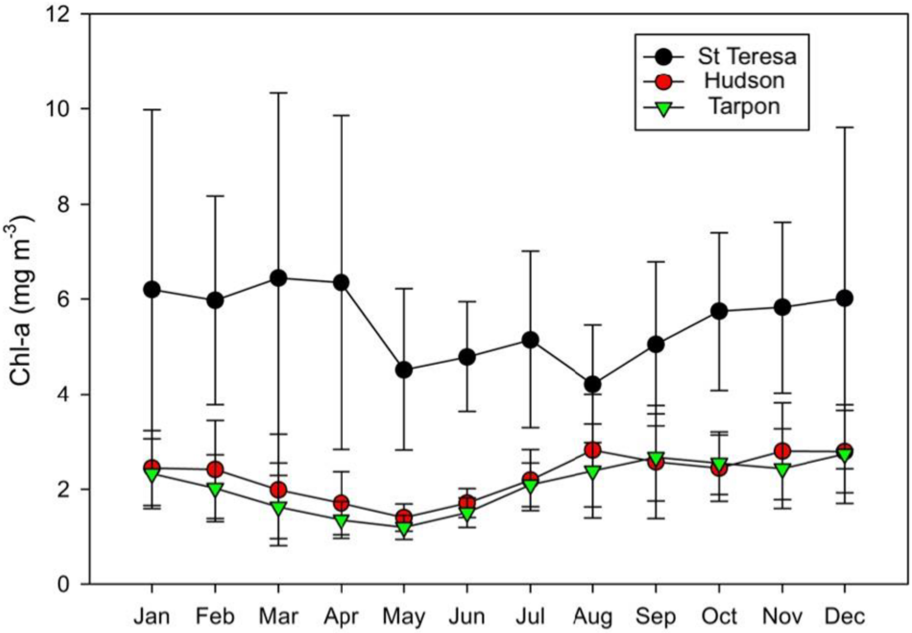

Figure 9. Monthly mean Chl-*a* values averaged over 2012–2020. Error bars show one standard deviation from the mean.

winter to early spring (Morey et al. 2009). River flow influences salinity, nutrients, plankton, and turbidity up to 200 km away (Morey et al. 2009). Discharge from the Apalachicola River has high concentrations of Chl-*a*, which contributes to higher Chl-*a* values in the St Teresa region compared to the other two regions (Fig. 9). High Chl-*a* is correlated with high phytoplankton abundances which make waters more turbid and reduce light levels, which affects the zooxanthellate photosynthesis. However, the high plankton and particulate concentration provides the corals with more food for heterotrophic feeding. For tropical corals, heterotrophic feeding has been shown to meet up to 15%–35% of daily carbon requirements for healthy corals, and up to 100% in bleached corals (Houlbrèque and Ferrier-Pagès 2009). For stony corals in general, heterotrophy can be an important source of energy that cannot be received from the symbiotic zooxanthellae. Due to the lower winter temperatures, higher sedimentation rates, and less light transmission of the Florida Panhandle as compared to the more southern regions, the corals live under conditions that would be considered stressful for tropical reef corals. These communities may be adapted to these apparently sub-optimal conditions, and/or the seasonal influx of nutrients and food from the Apalachicola River can support the growth of these dense coral communities. This is consistent with the findings in this study where the St Teresa region has higher abundances of corals, octocorals, and sponges than would be expected due to temperature alone.

When combined with the data from Walker et al. (2020), the differences observed during this study between the St Teresa, Hudson, and Tarpon regions were diminished. Data collected by Walker et al. (2020) grouped octocorals into morphological groups as opposed to the taxonomic groups used in this study. The morphological grouping provided lower resolution than the taxonomic groups, obscuring differences among the regions. This highlights the importance of high-resolution identification in community surveys, as the octocoral species and complexes were responsible for many of the differences between the Tarpon, Hudson, and St Teresa regions.

Coral sizes generally did not vary significantly throughout the study, with the exception of the Plexauridae which were significantly different between all three regions. The largest colonies occurred in Hudson and the smallest in St Teresa. This can be a function of different species within the complexes and/or local environmental and nutrition conditions. Additional taxonomic and environmental data is needed to determine the cause of these differences. Though Hudson had the largest colonies of Plexauridae octocorals, it had lower overall densities of octocorals and stony corals while percent cover remained similar to other regions.

Overall, the coral communities appeared healthy across the study area and no disease was observed. Fully bleached colonies were rare (<0.1% of total colonies), and the majority of bleaching observed was partial bleaching, such as the tips of *Oculina* and *S. hyades* colonies or paling in *S. radians* colonies. ANOSIM showed significant differences between regions but with a low R-value (R = 0.35), indicating that signs of bleaching may have a small effect on regional differences. *Solenastrea hyades* and *Oculina* spp. showed the highest prevalence of bleaching, which is consistent with a study by Eagan (2019) that showed these two species comprised 85% of the bleached colonies observed near Tampa Bay, Florida.

Harmful algal blooms (HABs), particularly of the dinoflagellate *K. brevis,* have occurred on the north and eastern Gulf of Mexico coasts since the 1800s, with blooms on the eastern Gulf being more frequent (Colella et al. 2008). *Karenia brevis* releases brevetoxins that, in high concentrations, can cause massive mortality events, particularly in fishes, turtles, and marine mammals (Brand et al. 2012). The toxins can also directly impact invertebrates, including corals (Ross et al. 2010). Indirect impacts to benthic communities can also occur when the large amounts of sinking organic matter decompose to create hypoxic conditions near the seafloor and expose benthic organisms to potentially lethal conditions (Turley et al. 2022). The spatial extent of these events varies, but multiple severe red tides have been recorded in the Tarpon and Hudson regions, most recently in 2014 (Pierce and Henry 2008, Karnauskas et al. 2019).

Demographic analyses found significantly larger stony coral colonies in 2021 than in 2017 over the same general area in Pasco County for three of the four species (Fig. 7). Coral communities on artificial reefs have been shown to recover within 4–5 yrs of red tide–related anoxia (Dupont et al. 2010). With the most recent red tide affecting the Pasco County area in 2014, the stony corals would have been three years removed in 2017 and seven years in 2021, allowing them more time to recover and grow to larger sizes.

Conclusions

This study surveyed hard bottom communities across the coastal WFS and identified three significantly different communities, two of which occur over a small spatial scale. The distinct communities found in this study are likely a result of one or a combination of local factors and influence from the BFZ and hydrodynamics of the coastal shelf. This study builds upon existing research on the coastal WFS and expands our understanding of the biogeography of the region. Though this study identified many octocorals to species level, several organisms thought to be of the *Eunicella*, *Plexaurella*, and *Psuedoplexaura* genera were grouped into the Plexauridae category due to the difficulty of identifying differences in polyp and spicule structure from video transects. Similarly, several species of *Muricea* may have been observed yet were indistinguishable from the video and were grouped together to avoid misidentification. Even with cautious taxonomic identifications, the three regions showed significantly different communities and it is possible that regional differences are more pronounced than shown in this study. The complexes may be comprised of different species in each region which would contribute to stronger differences in the community compositions. As shown when combining datasets, high resolution taxonomic identifications are needed to fully assess a community.

The timing of the surveys varied between the study regions, with summertime sampling for Hudson and St Teresa (June and August) and Tarpon Springs in winter (February). Though this study targeted sessile organisms that do not migrate with seasonal changes, abiotic and biotic factors such as temperature, visibility, algal dominance, etc. may potentially influence video analysis accuracy and/or the degree of coral bleaching. High turbidity and algal growth can potentially impact video quality and accuracy of analysis. During sampling there were several periods of suboptimal visibility, however, the cameras were still able to capture high quality images for accurate species and percent cover assessments. To address influences of algal cover on community assessments, algae was removed from quadrats prior to taking images. High temperatures or shading—due to high turbidity, Chl-*a*, or algal overgrowth—can cause stony coral bleaching. Sea surface temperatures were highest in August across all regions; however, Hudson saw more colonies with signs of bleaching than other regions when sampled in June. Chl-*a* was also lower in Hudson in June than in St Teresa in August. Higher bleaching and lower stony coral densities indicate that the Hudson region overall may be suboptimal for stony coral growth, despite more favorable environmental conditions during the sampling period than other sites.

We suggest surveying the region between Hudson and St Teresa to better characterize the extent of the potential ecoregion boundary or transition zone in that region and identify whether local factors or larger-scale circulation may be responsible for the distinct communities. A concentrated effort to streamline taxonomy and expand in situ identification training is needed to be able to conduct high resolution community surveys, as spicule analysis and/or genetic sequencing is not possible for all organisms in a study area. Hard bottom coral communities are essential fish habitats that provide nursery and feeding grounds for commercially important fish species, yet information on them is minimal in this region. These findings highlight the need for further community analysis across a larger expanse to create a comprehensive and detailed understanding of benthic hard bottom communities of the WFS.

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