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Rebekah Rodriguez

University of Texas Rio Grande Valley, rebekahrodriguez87@gmail.com

Erin E. Easton

University of Texas Rio Grande Valley, erin.easton@utrgv.edu

Thomas C. Shirley

Texas A&M University-Corpus Christi, thomas.shirley@tamucc.edu

John W. Tunnell

Harte Research Institute for Gulf of Mexico Studies

David Hicks

University of Texas Rio Grande Valley, david.hicks@utrgv.edu

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PRELIMINARY MULTIVARIATE COMPARISON OF CORAL ASSEMBLAGES ON CARBONATE BANKS IN THE WESTERN GULF OF MEXICO

Rebekah Rodriguez¹, Erin E. Easton¹, Thomas C. Shirley², John W. Tunnell, Jr.³, and David Hicks^{1,*}

¹University of Texas Rio Grande Valley, School of Earth, Environmental, and Marine Sciences, Brownsville, TX 78520; ²Department of Life Sciences, Texas A&M University–Corpus Christi, Corpus Christi, TX 78412-5800; ³Harte Research Institute for Gulf of Mexico Studies, Texas A&M University–Corpus Christi, TX 78412-5869; *Corresponding author: david.hicks@utrgv.edu

ABSTRACT: Hermatypic corals flourished on reefs in the Gulf of Mexico (GOM) in the late Pleistocene and early Holocene. Today, many of these relict reefs are mesophotic banks that have unique coral assemblages and provide critical habitat; however, the South Texas Banks (STB) lack quantitative surveys. Therefore, we used a remotely operated vehicle to conduct quantitative surveys of 5 banks: Baker, Aransas, Dream, Blackfish Ridge, and Harte. Coral communities, based on estimated coral densities (colonies/m²), significantly differed among banks for terraces, slopes, and overall (combined terrace and slope) communities for most banks examined. Within banks, terrace and slope communities significantly differed for all banks except Harte. Sea whips were the most abundant group on slopes and terraces of most banks and frequently contributed >50% to community similarities and dissimilarities, whereas sea fans and *Antipathes* frequently contributed >20%. Total coral abundance was twice as high and sea fans were 7 times more abundant on terraces than slopes. Among-bank differences in coral communities were highly correlated to geographic and geomorphic features, especially to bank area, rugosity, longitude, and number of site components. The drivers of these differences, their effects on ecosystem diversity and function, and the connectivity pathways within and among STB and other GOM banks require further investigation. Nevertheless, the observed diversity in community structure within and among banks should be considered in the development of monitoring, conservation, and management plans of these critical habitats.

KEY WORDS: mesophotic, coral banks, benthic communities, ecology, South Texas Banks

INTRODUCTION

At mesophotic depths along the Gulf of Mexico (GOM) shelf, natural hard-bottom habitats are sparse and intermittently distributed. In the northwestern GOM, these habitats can be divided, based on their geologic origin, into 2 regions extending east and south of Matagorda Bay (Nash et al. 2013): (1) Salt Diapir Banks that formed from sheets of allochthonous salt and (2) South Texas Banks (STB) that formed from relict carbonate reefs (Belopolsky and Droxler 1999, Weaver et al. 2009, Khanna et al. 2017). Biodiversity of reef-building and other structure-forming fauna on these banks differs with depth and physical structure (Rezak et al. 1983, Hickerson et al. 2008). Shallow banks (<50 m) are active reef-building areas dominated by hermatypic corals with abundant crustose coralline algae (CCA) and limited leafy algae, whereas deep banks (>50 m) have limited reef-building activity and are characterized by sponges, ahermatypic corals, and CCA, with CCA dominance decreasing with depth. On the western GOM shelf at depths below 70 m, reef-building activities can be impeded by a persistent zone of high turbidity, sedimentation, and resuspended sediment (nepheloid layer) that can be over 35 m thick (Rezak et al. 1983, Hickerson et al. 2008).

Reefs and banks at 30–150 m that have light-dependent zooxanthellate corals that can thrive in low-light conditions are referred to as mesophotic coral reef ecosystems (MCEs) (Lesser et al. 2009, Kahng et al. 2010). In addition to zooxanthellate corals, azooxanthellate corals, sponges, CCA, and macroalgae dominate MCEs and provide habitat for a diversity of fauna. Mesophotic coral ecosystems sup-

port higher abundances and diversity of invertebrate and fish communities compared with surrounding soft bottom habitats, serve as spawning grounds for many fishes, and may provide a refuge for shallow and mid-depth species (Rezak et al. 1983, Thompson et al. 1999, Pyle 2000, Lesser et al. 2009, Tunnell et al. 2009, Bongaerts et al. 2010). Despite the ecological importance of MCEs, knowledge of their importance, diversity, and richness has advanced only recently (Kahng et al. 2014, Pyle et al. 2016) but quantitative studies of STB communities are limited.

In the 1970s and 1980s, researchers surveyed 11 of the STB, reported non-quantitative species lists, and characterized the topography, geological composition, regional and local current regimes, temperature, salinity, and river influences on turbidity at the surveyed banks (Abbott and Bright 1975, Bright and Rezak 1976, Rezak et al. 1983, Dennis and Bright 1988, Rezak et al. 1990). After the establishment of marine protected areas (MPAs) to protect and manage critical ocean resources increased and consequently led to renewed interest in the STB (Weaver et al. 2006, Tunnell et al. 2009, Nash et al. 2013, Hicks et al. 2014), additional STB surveys were conducted in 2006, 2008, and 2012 to provide data to inform management decisions. These surveys revealed that STB fish communities include an unusual assortment of deep-water and tropical, shallow-water species and that ahermatypic coral species, in particular antipatharians interspersed with octocorals, and CCA dominated the terraces and upper slopes of the STB. These surveys revealed that the STB provide critical ecological services (e.g., feeding hab-

itat, shelter, and spawning grounds) for invertebrates and fishes but the STB have little protection from human activities. For example, only 9 STB have limited protection from energy–extraction activities. These protections include no–activity zones on their upper slopes and terraces with some banks also having 1000 m stipulation zones for drill cuttings and fluids (BOEM 2015). In contrast, other topographic features in the northwestern GOM have larger no–activity zones with 3 mile stipulation zones in addition to fisheries–related protections (BOEM 2015).

The full extent of the services the STB provide has not been assessed because information on their communities and physical settings is limited (Weaver et al. 2006, 2009b, Puglise et al. 2009, Tunnell et al. 2009). For example, quantitative surveys of the coral communities have not been reported. Such information is especially critical under current threats to shallow and deep coral ecosystems and the limited information on MCEs and the effects of natural and anthropogenic disturbances (Puglise et al. 2009, Bridge et al. 2013, Appeldoorn et al. 2016). To fill this knowledge gap, we conducted the first quantitative surveys of the STB and characterized the coral communities of 5 mid–shelf banks: Baker, Aransas, Dream, Blackfish Ridge, and the previously unsurveyed Harte Bank (Figure 1). The objectives were to (1) identify and quantify coral groups on the studied banks, (2) compare coral communities among banks and between topographic features (i.e., slope and terrace), and (3) determine which physical descriptors (e.g., area, rugosity, number of terraces) best explain the observed coral community patterns.

MATERIALS AND METHODS

Data collection

In September 2012, video transects were conducted from the RV *Falkor* (Schmidt Ocean Institute) with the remotely operated vehicle (ROV) Global Explorer MK3 (Oceaneering® International, Houston, TX). The ROV was equipped with a multi–jointed hydraulic manipulator arm, 2 thermally insulated drawers, 4 semi–conducting parallel lasers at a fixed separation of 10 cm, and an Ocean ProHD Camera System (Oceaneering® International) with 2 front–facing 3X cameras. Reference information, e.g., depth, altitude, time, and position, was overlaid on video from one camera recording at 720 progressive scan and 60 f/s. During transects, the

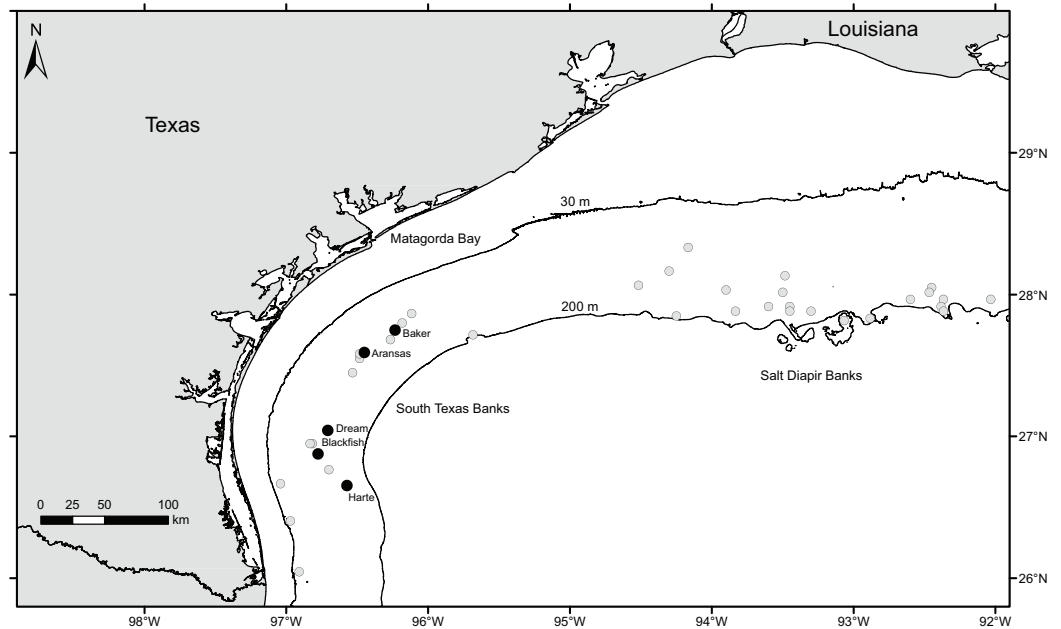


FIGURE 1. The location of the 5 studied banks (black circles) and other known banks (grey circles) between 30 and 200 m in the northwestern Gulf of Mexico. Modified from Nash et al. 2013.

ROV maintained a consistent height (~1 m) and speed (~0.1 m/s) above the seafloor, and the second camera, recording at 1080 interlaced scan with a 105° viewing angle, was oriented at 160° tilt to capture video for benthic community analyses. The position of the ROV was tracked with a Ranger 2 Subsea USBL positioning system (Sonardyne International, Yateley, UK), and position data were translated into NMEA format using HYPACK® (Xylem, Middleton, CT). Temperature, conductivity, pressure, salinity, and sound velocity were measured with a SBE 37–SI MicroCAT C–TP recorder (Sea–bird Scientific, Bellevue, WA) attached to the ROV.

Bank and transect descriptions

Each bank was first mapped with an EM® 710 multibeam echosounder (Kongsberg Maritime, Kongsberg, Norway) before conducting, depending upon bank size and morphology, one or 2 ROV transects that generally extended from the base to the terrace of each bank. Banks surveyed in this study were described in detail in Nash (2013, 2014), Hicks et al. (2014), and Khanna et al. (2017). In brief, Baker Bank is a 1.39 km² rectangular feature with a vertical relief of 16 m (Figure 2A). We conducted 2 discrete transects, each ascending to the terrace at 60 m from 73 m and 76 m at the northern and southern bases, respectively. Combined, the 2 transects covered a linear distance of 450 m. Aransas Bank is a 0.51 km² circular feature with a vertical relief of 14 m (Figure 2B). We conducted one transect of 564 m ascending from 69 m to the terrace crest at 60 m before descending the opposite slope to 69 m. Dream Bank is a 2.07 km² elliptical feature with a vertical relief of 16 m (Figure 2C). One transect of 1,100 m extended across the terrace crest at 69 m from the slope base to the slope base at 82 m (north side) and 84 m (south side). Blackfish Ridge is a 1.36 km² elliptical

cal feature with a vertical relief of 14 m (Figure 2D). One 270 m transect ascended from the northside base at 73 m to the crest at 62 m. Harte Bank is a 0.37 km² rectangular feature with a vertical relief of 16 m (Figure 2E), and was surveyed using one transect of 394 m, extended across the terrace at 83–90 m from the slope base at 99 m.

Video analysis

DVMP Pro 5 software was used to embed time–stamp metadata on each video. The ~36 h of videos were reviewed in their entirety to eliminate frames when the ROV was at rest or too far from the seabed to accurately assess the macrofaunal community, the video was out of focus, or the parallel lasers were not present. For each transect, the video was then spliced and 30 second sequences were subsampled with Ultra Video Splitter (Aone Software). Subsampled sequences were classified as slope or terrace habitat. The linear distance between the start and end position of each sequence was considered the length of the subsampled sequence and was derived from the simplified inverse geodetic equation (Vincenty 1975, Karney and Deakin 2010) with equatorial and polar radii of 6,378,200 and 6,356,750 m, respectively. This distance and the mean width of the field of view, estimated from the parallel lasers, were used to estimate the area surveyed (m²) in each sequence.

Coral species were identified to the lowest possible taxon with the aid of original species descriptions and the NOAA Flower Garden Banks National Marine Sanctuary image and document library (<https://flowergarden.noaa.gov>). Colonies of *Antipathes furcata* and *Thelogorgia stellata*

could be assigned consistently to species based on their distinct morphology. Because of difficulty in identifying corals to species on the basis of video data, all other colonies could not be consistently assigned to species, genera, or in some cases family. To maximize the number of groups and therefore detail obtained from the analysis, we assigned all other colonies to the lowest possible groupings in which we had confidence that errors in identification did not occur: *Tanacetipathes*, *Antipathes* (except *A. furcata*), *Hexacorallia*,

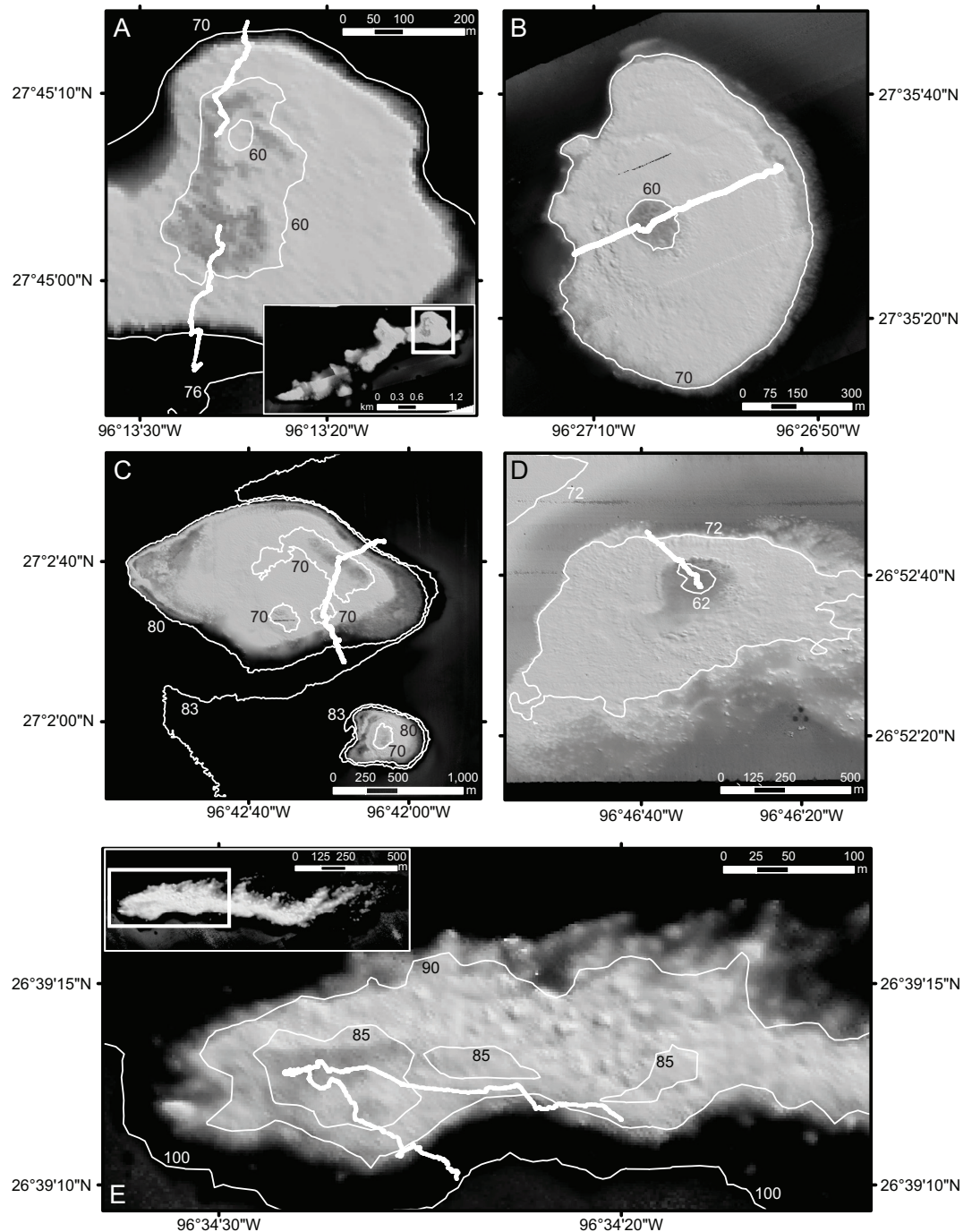


FIGURE 2. Charts indicating transect locations (thick white lines) and select depth contours (thin white lines) in meters at the terrace and base of 5 banks in the northwestern Gulf of Mexico. A. Baker Bank. B. Aransas Bank. C. Dream Bank. D. Blackfish Ridge. E. Harte Bank. The extent of Baker Bank (A) and Harte Bank (E) are indicated by the white-outlined boxes in the insets.

TABLE 1. Bank and transect characteristics. Distance to nearest neighbor, regional depth, shallowest depth, rugosity, terrace count (*Ter*), and number of site components (*Site comps*) were determined by Nash et al. (2013).

	Bank							Transect					
	Lat (N)	Long (W)	Bottom temp (°C)	Nearest Neighbor (km)	Regional depth (m)	Shallowest depth (m)	Area (km ²)	Rugosity	Ter	Site comps	Date (2012)	Length (m)	Depth (m)
Aransas	27.592	96.450	23.5-24.1	3.08	73	59	0.51	0.00143	4	1	19-Sep	564	60-69
Baker	27.750	96.233	23.7-23.8	9.22	74	58	1.39	0.00187	3	5	21-Sep	451	60-76
Blackfish	26.877	96.777	23.1-23.8	9.26	75	61	1.36	0.00154	3	1	23-Sep	270	62-73
Dream	27.042	96.708	22.8-25.7	14.55	84	68	2.07	0.00129	4	2	26-Sep	1100	69-84
Harte	26.654	96.573	19.9-23.0	17.96	99	83	0.37	0.00324	2	3	27-Sep	394	83-99

sea fan, sea whip, and hydroid. Coral colonies, characterized as a single-stemmed organism, were counted as they crossed the bottom of the viewing frame and densities (colonies/m²) were calculated for each species per video sequence.

The following abiotic variables were calculated by Nash (2013) and used in this study: distance to nearest neighbor, regional depth, shallowest depth, area, rugosity, terrace count, latitude, longitude and number of site components (Table 1). In brief, distance to nearest neighbor was determined from the center peak coordinates of each bank and the Haversine formula for great-circle distances of a sphere. Regional depth was the mean depth of a 200 m buffer zone outside polygons defining the boundary at the base of each site component in ArcGIS®, while shallowest depth was the depth at the crest/peak. Area was the planimetric area of the defined site components, rugosity was calculated using the Benthic Terrain Modeler version 3.0 (Walbridge et al. 2018), and terrace count was defined as the number of flat areas bounded by steep slopes. Latitude and longitude were the center peak coordinates, and number of site components was defined as the number of individual geologic structures within the bank boundary.

Statistical analyses

Because of unbalanced sample sizes, we used all subsampled sequences from Blackfish Ridge, Harte Bank, and Baker Bank slope, which had ≤ 30 subsamples per topographic feature (i.e., slope and terrace), and we randomly selected 30 subsamples from those banks with > 30 subsampled sequences per topographic feature. Sample rarefaction curves (Figure S1), produced with PAST v. 3.20 (Hammer et al. 2001), indicated that 30 subsamples is sufficient to capture 5.5 of 6 and 7.2 of 8 groups recorded on the slopes and terraces, respectively. On slopes, 10 subsamples were sufficient to capture 4.5 of the 6 groups. Subsamples totaled 38.8% (Aransas), 27.3% (Baker), 59.8% (Blackfish), 21.2% (Dream), and 31.2% (Harte) of the total transect area per bank. Non-parametric analyses were conducted in Primer v. 7.0.13 (Clarke 1993, Clarke et al. 2014, Clarke and Gorley 2015). Densities were fourth-root transformed and Bray-Curtis

similarities among samples were calculated. To test for differences in community structure among banks and topographic features, we analyzed the data using a 2-way, crossed PERMANOVA with bank and topographic feature as fixed factors with 9999 permutations. Default settings were: Sum of Squares = Type III, fixed effects sum to zero for mixed terms = checked, and permutation method = permutation of residuals under a reduced model. Because significant interaction was detected among factors, follow-up pairwise tests comparisons were conducted for the bank x topographic feature term. Differences detected by PERMANOVA can be attributed to location effects and dispersion effects of samples. To determine if observed differences were, in part, because of dispersion effects, we conducted a PERMDISP analyses with the following settings: 9999 permutations, pairwise tests, and distance to centroids. The correlated Bonferroni technique (Drezner and Drezner 2016) was applied to control for potential type I error associated with multiple testing.

To identify which taxa contributed the most to similarities/dissimilarities among topographic features and banks, we conducted the following SIMPER analyses with pairwise comparisons: two-way crossed analysis with bank and topographic feature as factors and one-way analysis on “bank x topographic feature” as the factor. We used the BEST routine to determine which abiotic variables best explained patterns in community structure; for highly correlated (> 0.95) variables, only one variable was used in the analysis. Only regional depth and shallowest depth were highly correlated (0.996); shallowest depth was retained in the analysis because it is considered more important in influencing biodiversity along the STB (Nash et al. 2013). Because abiotic variables were determined for each bank and not for topographic features, the analyses were based on mean coral densities for each bank. As above, these mean density values were fourth-root transformed prior to calculating Bray-Curtis similarities. Abiotic variables were normalized prior to running the BEST routine with the following parameters: rank correlation method = Spearman, method = BIOENV, maximum number of trial variables = 5, Resemblance measure =

Euclidean distance, maximum number of best results = 10, and permutations = 9999. To assess similarity in community structure among banks, terraces, and slopes, we performed ordination by using non-metric multidimensional scaling (nMDS) analyses with default settings on the similarity matrices calculated from the complete data set and from the mean coral densities by bank.

RESULTS

From ~36 h of video, we subsampled 497 sequences; 157 were categorized as slope and 340 as terrace. Fewer slope sequences were quantified due to higher amounts of resuspended sediment and therefore lower-quality video for slopes compared with terraces. Although assigning corals to species on the basis of video data limited our ability to assign all colonies consistently to species, genera, or in some cases family, we can provide probable species included in our coral groups based on morphological and genetic analyses (unpubl. data) of colonies collected at these banks. These data indicate that the majority of sea whips were likely the antipatharian *Stichopathes lutkeni* with some *S. cf. occidentalis* and *Ellisella* spp. Sea fans included *Bebryce cinerea*, *Scleraxis cf. guadalupensis*, *Hypnogorgia pendula*, and *Placogorgia* spp., among others. *Antipathes* consist primarily of *A. atlantica*; however, some may be *A. gracilis*. Hexacorallia primarily included species in the families Oculinidae and Pocilloporidae, e.g., *Madraxis brueggemanni*. *Tanacetipathes* included *T. barbadensis* but likely also *T. hirta*, *T. tanacetum*, and *T. thamea*. This report is the first for *Thelogorgia stellata* and *Tanacetipathes barbadensis* at the STB; the former was identifiable from video and both were identified by morphological analyses of collected specimens.

Community structure significantly differed by bank and topographic feature, with significant interaction between these factors (Table 2). Pairwise testing on the term “bank x topographic feature” revealed that community structure significantly differed among (1) terraces for all banks, (2) slopes between Harte and all other banks and between Blackfish and Dream, and (3) slopes and terraces within all banks except Harte Bank (Table S1). PERMDISP indicated that dispersion significantly differed among factor states (Table 2), but only 26.3% of significant pairwise PERMANOVA comparisons had significantly different pairwise dispersion (Table S1). These results, examination of dispersion in MDS plots, and comparison of within-group and between-group similarities indicate that significant differences are largely due to location effects, i.e., differences among banks and topographic features.

Except for Harte Bank, overall within- and among-bank similarities were relatively low (41.5–58%, 70.3% for Harte Bank, Table 3); terrace similarities (42.9–67.4%, 71.6% for Harte Bank) within and among banks were high compared to slope similarities (12.3–49.2%, 62.3% for Harte Bank) within and among banks (Table 3). Sea whips were the most

abundant group (0.8–2.4 colonies/m²) on slopes and terraces of most banks; sea fans, *A. furcata*, and *Antipathes* were usually the next-most abundant groups (Table 4). These groups

TABLE 2. Statistical results of the 2-way, crossed PERMANOVA (9999 permutations) with fixed factors Bank and Topographic feature (i.e., slope and terrace), Type III (partial) sum of squares, and permutation of residuals under a reduced model. PERMDISP was run with distances from centroids and 9999 permutations run in Primer v. 7.0.13. na = not applicable. Perms = number of unique permutations.

	df	SS	MS	Pseudo-F	P	Perms
PERMANOVA						
Bank	4	23530	5882.6	11.782	0.0001	9930
Topographic feature	1	16038	16038	32.122	0.0001	9961
Bank x Topographic feature	4	8338.6	2084.6	4.175	0.0001	9942
PERMDISP						
Bank	4, 227	na	na	8.220	0.0002	na
Topographic feature	1, 230	na	na	0.309	0.6128	na
Bank x Topographic feature	9, 222	na	na	3.330	0.0054	na

TABLE 3. Coral community similarities among banks, terraces, and slopes.

	Bank similarities					
	Aransas	Baker	Blackfish	Dream	Harte	All
Aransas	52.76					
Baker	52.49	57.97				
Blackfish	52.89	48.38	56.06			
Dream	44.79	44.39	46.35	48.54		
Harte	54.25	41.48	53.16	41.67	70.33	
All						40.78
	Terrace similarities					
	Aransas	Baker	Blackfish	Dream	Harte	All
Aransas	67.4					
Baker	55.77	58.5				
Blackfish	57.78	49.79	57.83			
Dream	51.58	45.99	48.18	52.15		
Harte	60.24	42.86	55.31	47	71.64	
All						60.75
	Slope similarities					
	Aransas	Baker	Blackfish	Dream	Harte	All
Aransas	37.6					
Baker	25.1	12.25				
Blackfish	43.3	27.19	49.2			
Dream	37.72	31.01	42.76	44.79		
Harte	39.88	16.67	43.16	28.91	62.3	
All						42.85

contributed the most, frequently > 20%, to community similarities and dissimilarities (Table S2); sea whips frequently contributed > 50%. Total coral abundance was twice as high and sea fans were 7 times more abundant on terraces than slopes (Table 4). Hexacorallia were unique to the Baker Bank terrace (Table 4).

BEST identified the 4 variable model with area, rugosity, longitude, and number of site components as the best model to explain patterns in coral community structure among banks ($\rho = 0.83$, $p = 0.163$). The best models for one to 5 variables are reported in Table S3; rugosity was the best one variable model ($\rho = 0.58$). The high correlation between the selected model and the coral community structure is apparent in the strong concordance between nMDS ordination of the BEST abiotic variables and that of the biotic variables (Figure 3).

DISCUSSION

Comparisons to previous surveys

This report of STB coral communities is the first one in over 20 years for the STB and the first for Harte Bank (see Nash et al. 2013 for a review of fauna surveys for the STB); unlike previous surveys, our report is quantitative. The banks surveyed in this study have similar coral community compositions to those surveyed in the 1970s and 1980s (Rezak et al. 1983), i.e., they are dominated by *Antipathes*, sea whips (in particular *Stichopathes* spp.), and large white sea fans (i.e., *Hypnorgia pendula*). We did identify 2 species

that, although reported for the GOM (Brooke and Schroeder 2007, Etnoyer and Cairns 2017), had not previously been reported for the STB: *Thelogorgia stellata* and *Tanacetipathes barbadensis*. These new reports are possibly due to different sampling efforts between this study and those of the 1970s and 1980s.

Coral densities at the surveyed banks are comparable to those in the southern GOM. For example, *Antipathes* and *A. furcata* densities were respectively 0.0–0.8 and 0.0–1.4 colonies/m², which is comparable to banks along the Mexican coast, where mean black coral (*A. pennacea* and *A. caribbeana*) densities are 0.1–0.5 colonies/m² at banks impacted by fisheries and up to 1.3 colonies/m² at less impacted sites (Pardilla and Lara 2003). Although sea whips can achieve densities up to 10–20 colonies/m² for mesophotic banks and mid–depth seamounts (550–1150 m), their densities are often considerably lower (Genin et al. 1986, Opresko and Genin 1990, Bo et al. 2009). In this study, mean sea whip densities were 0.8–1.6 colonies/m² for terraces and slopes, except for Baker bank terrace, where densities were substantially higher at 2.4 colonies/m².

Sedimentation and the nepheloid layer can have negative effects on coral and algal communities of the GOM banks by reducing light penetration and smothering epibenthos (Rezak et al. 1983, Rezak et al. 1990, Gittings et al. 1992, Tunnell et al. 2009). For example, Gittings et al. (1992) found that invertebrate assemblages on outer continental

TABLE 4. Mean densities (colonies/m²) and standard errors for each coral group. Values in parentheses indicate the number of subsampled video sequences. NP = not present.

	<i>Antipathes</i>	<i>A. furcata</i>	Hexacorallia	Hydroids	Sea fans	Sea Whips	<i>Tanacetipathes</i>	<i>Thelogorgia stellata</i>
Aransas Bank (60)	0.15 ± 0.03	0.14 ± 0.03	NP	0.05 ± 0.03	0.30 ± 0.07	1.53 ± 0.22	0.03 ± 0.01	NP
Slope (30)	0.18 ± 0.06	0.05 ± 0.02	NP	0.02 ± 0.02	0.09 ± 0.05	1.45 ± 0.38	0.01 ± 0.00	NP
Terrace (30)	0.12 ± 0.04	0.23 ± 0.06	NP	0.08 ± 0.06	0.51 ± 0.12	1.61 ± 0.21	0.05 ± 0.02	NP
Baker Bank (34)	0.04 ± 0.01	0.06 ± 0.02	1.52 ± 0.77	0.13 ± 0.07	0.61 ± 0.15	2.30 ± 0.37	0.01 ± 0.01	NP
Slope (4)	NP	NP	NP	NP	NP	1.37 ± 1.30	NP	NP
Terrace (30)	0.04 ± 0.02	0.06 ± 0.03	1.73 ± 0.87	0.15 ± 0.08	0.69 ± 0.17	2.43 ± 0.38	0.01 ± 0.01	NP
Blackfish Ridge (44)	0.44 ± 0.08	0.15 ± 0.05	NP	0.28 ± 0.12	0.52 ± 0.20	1.16 ± 0.13	0.01 ± 0.01	NP
Slope (15)	0.25 ± 0.10	0.15 ± 0.13	NP	NP	0.28 ± 0.25	0.88 ± 0.21	0.03 ± 0.02	NP
Terrace (29)	0.53 ± 0.10	0.15 ± 0.05	NP	0.42 ± 0.18	0.64 ± 0.28	1.30 ± 0.17	NP	NP
Dream Bank (60)	0.14 ± 0.03	0.05 ± 0.02	NP	0.04 ± 0.02	0.80 ± 0.31	0.81 ± 0.15	NP	NP
Slope (30)	0.03 ± 0.02	NP	NP	NP	0.04 ± 0.02	0.84 ± 0.20	NP	NP
Terrace (30)	0.26 ± 0.06	0.11 ± 0.03	NP	0.09 ± 0.03	1.56 ± 0.60	0.79 ± 0.21	NP	0.01 ± 0.01
Harte Bank (34)	0.80 ± 0.11	1.40 ± 0.15	NP	0.02 ± 0.01	0.12 ± 0.03	1.50 ± 0.40	0.03 ± 0.02	NP
Slope (10)	0.78 ± 0.21	0.82 ± 0.16	NP	NP	0.11 ± 0.06	1.42 ± 0.34	0.07 ± 0.05	NP
Terrace (24)	0.81 ± 0.14	1.65 ± 0.18	NP	0.02 ± 0.01	0.12 ± 0.03	1.54 ± 0.55	0.01 ± 0.01	NP
All slopes (89)	0.20 ± 0.04	0.13 ± 0.04	NP	0.01 ± 0.01	0.10 ± 0.05	1.14 ± 0.16	0.02 ± 0.01	NP
All terraces (143)	0.33 ± 0.04	0.39 ± 0.06	0.36 ± 0.19	0.15 ± 0.04	0.73 ± 0.15	1.54 ± 0.15	0.02 ± 0.00	NP

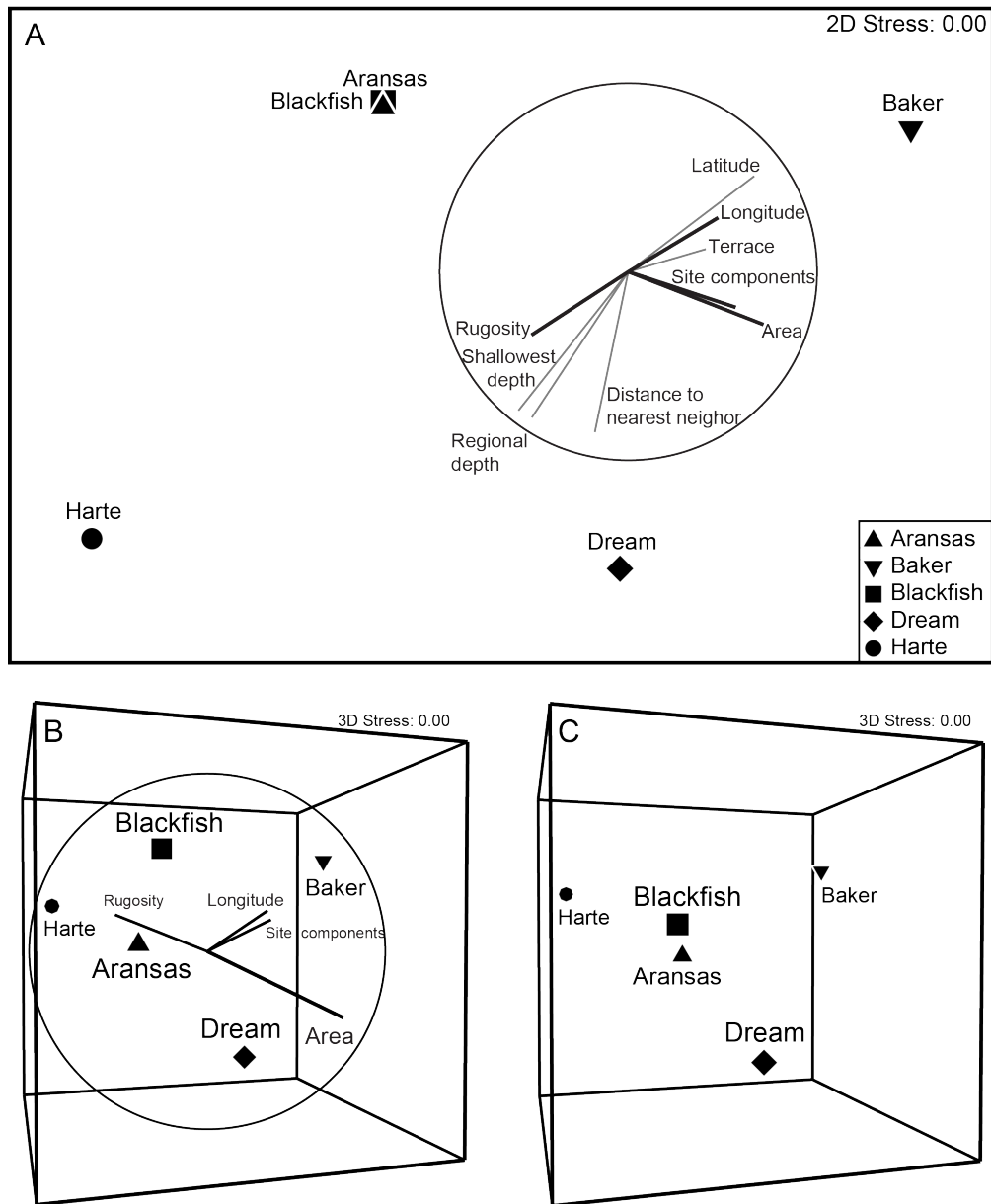


FIGURE 3. nMDS ordination of South Texas banks showing a clear separation in coral communities among banks. A. Two-dimensional and B. 3-dimensional nMDS ordinations of banks based on the Bray-Curtis similarities of fourth-root transformed mean coral densities. C. Three-dimensional nMDS ordination of banks based on Euclidean distances of the 4 abiotic variables identified by the BEST routine in Primer as the best model to explain patterns in coral community structure among banks ($\rho = 0.83$, $\rho = 0.163$). The high correlation between the selected model and the coral community structure is apparent in the strong concordance between nMDS ordination of these best-explaining abiotic variables (C) and that of the biotic variables (B). Pearson correlations of all abiotic variables to the nMDS axes are indicated by the superimposed vectors on A, with the variables identified by BEST **bolded** and overlaid on B. The circle indicates a correlation of 1.

shelf banks along the northern GOM from eastern Louisiana to Alabama were influenced by sedimentation associated with the Mississippi River plume. On these banks, coral aggregations were scarce on structures near the plume and increasingly common with distance from the plume. For the STB, species diversity and abundance are lower on low-relief banks and banks exposed to high turbidity and the nepheloid layer (Rezak et al. 1983), which is highly variable in the GOM. Compared to banks affected by the Mississippi River plume, the banks of the STB experience less sedimentation. Sediment runoff between the Brazos–Colorado and Rio Grande deltas is minor due to water diversions and flow-restricting structures (Rezak et al. 1983). The nepheloid layer and sedimentation affecting the STB is maintained by sea-floor turbulence, including disturbances from commercial fishing activities, and subsequent resuspension of sediments (Shideler 1981). Although we observed a relatively small

amount of suspended sediment at all surveyed banks except on the slope of Baker Bank, we did not quantify suspended sediments during this study. Therefore, we could not test for correlations between the sedimentation associated with the nepheloid layer and coral density and diversity. Future studies could evaluate whether significant differences in coral abundance and diversity among banks are correlated with sedimentation, especially for slope communities, which are more likely to be exposed to suspended sediments.

Community assemblages and structure

Coral densities on mesophotic reefs and banks are influenced by depth, substrate type and inclination, bottom topography, sediment loads, suspended food availability, and current and light availability (Sánchez 1999, Bo et al. 2009). For example, significant differences in community assemblage and coral densities exist between slopes and terraces of deep banks with some species predominantly inhabiting

only slopes or terraces, whereas other species inhabit both features (Sánchez et al. 1998, Sánchez 1999, Bo et al. 2009). Some antipatharians can be common in areas with relatively large quantities of suspended matter and azooxanthellate octocorals are common in areas with relatively high water flow (Sánchez 1999, Opreško and Sanchez 2005). When mean densities were calculated across all slopes and terraces in this study, coral densities were 1.3–15.0 times more abundant on terraces than slopes for all coral groups except *Tanacetipathes* and *Thelogorgia stellata*; however, the opposite pattern was observed for some groups and banks. Community structure also significantly differed between slopes and terraces for all banks except Harte. The primary contributors to these differences varied by bank and topographic feature; sea whips, sea fans, *Antipathes*, *A. furcata*, hydroids, and Hexacorallia contributed up to 39% to dissimilarities. Because we only had environmental data at the bank level, future studies are necessary to determine which abiotic factors (e.g., substrate inclination, sediment load, food availability, and dominant current flows) are driving these patterns with topographic feature, and whether these patterns would change if explored at the species level.

Among banks, the previously mentioned abiotic factors as well as geographic location, relative isolation, depth, rugosity, and habitat complexity of banks may control coral densities and drive differences in diversity and abundance of coral communities. For example, in habitat suitability models, Silva and MacDonald (2017) found that rugosity and, to a lesser extent, topographic position index, were the best predictors to explain sea fan and sea whip distributions on mesophotic banks of the eastern GOM. The best predictors of coral distribution at the species level were rugosity, bottom velocity, fraction of loose sediment, and topographic position index, which is considered a measure of preference to topographically intensified currents (Wilson et al. 2007). In this study, terrace and overall bank community structures differed significantly among most banks independent of topographic feature. The environmental variables that best explained the observed differences in community structure among banks were longitude, area, rugosity, and number of site components. The latter 3 variables are measures of habitat availability and complexity and are consistent with substrate and geomorphology being the best predictors of coral distribution on mesophotic and deep banks (Howell et al. 2011, Silva and MacDonald 2017).

A noteworthy consequence of the morphospecies strategy we used, i.e., assigning specimens to groups and not species,

is that it forces communities to be more similar than they may actually be. Therefore, it is important to examine which groups are the primary contributors to differences and identify which abiotic factors affect their density and distribution patterns. In this study, no one group was consistently the primary contributor to among-bank, among-terrace, and among-slopes differences although *A. furcata* was generally more abundant on terraces than slopes and contributed 11–40% to among-bank differences while sea whips contributed 20–56% to among-slope differences. These differences are likely related to the species-level effects of geomorphology and other abiotic factors at within- and among-bank scales. Such within-bank factors require further study at the STB before their effects on the observed coral distribution patterns can be explored.

Broader implications

Biodiversity studies in the northwestern GOM have primarily focused on coastal ecosystems near academic, federal, and state laboratories; protected areas; slope and deep-sea ecosystems associated with gas and oil exploration and production; and select economically important species (Fautin et al. 2010). In contrast, few investigations have been conducted on hard-substrate continental shelf ecosystems such as the South Texas coast, and few of these are quantitative. Therefore, the role of the STB in the system-wide ecology of the GOM remains unclear. This study was the first quantitative survey of the coral communities inhabiting the STB, so it produced critical baseline data for future studies and management decisions. Although not quantified, we did observe evidence of anthropogenic activity at some banks. For example, fishing wire, ropes, aluminum cans, and large unidentified steel objects were observed on the transects, and several sea fan skeletons were overgrown with zooanthids colonies at Harte Bank (personal observation, RR). Therefore, a monitoring program to determine the extent of damage and the overall ecosystem health is advised. Although the Gulf of Mexico Science Forum discussed the National Oceanic and Atmospheric Administration (NOAA)'s "Island in the Stream" concept and identified the STB as a potential site of a Marine Protected Area (Ritchie et al. 2008), the STB were removed from consideration because basic information about the relict reefs was lacking. This decision highlights the need and urgency to make this information known. Protection of these geological legacies should be considered further, particularly given evidence of anthropogenic debris and intra- and inter-bank differences noted during this study.

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