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# Patterns of Mesophotic Benthic Community Structure on Banks Off vs Inside the Continental Shelf Edge, Gulf of Mexico

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**Information on the biodiversity and geographic patterns of mesophotic, sessile, epibenthic communities on banks around and at the edge of the continental shelf, northern Gulf of Mexico, has been limited. These communities vary in their environments and are prone to disturbance from Outer Continental Shelf oil- and gas-related activities and fishing (trawling and long-lining). We surveyed these communities on the flanks of 13 banks to determine species richness, species composition, similarities between benthic communities, and geographic patterns in community structure. We sampled to ≤ 181 m in depth via a remotely operated vehicle using a vertically mounted digital camera bearing two lasers for scale and a flash (generally 10 drop-sites/bank, 5 transects/drop-site, and ≤11 photos/transect). Data analysis via PATN revealed three main Bank Groups: the on-shelf group containing 29 Fathom and Sonnier Banks; an anomalous bank—Geyer Bank; and the shelf edge group—Horseshoe, 28 Fathom, Bright, Alderdice, Bouma, Rankin, Rezak, Elvers, McGrail, and Sidner Banks. Most species-rich banks (Bank Group 3) occurred at the shelf edge. Two of the species-poor banks (Bank Group 1) occurred further north, inside the shelf. Geyer Bank (Bank Group 2) occurred at the shelf edge but was anomalously species-poor. Box-and-whisker analyses identified four Species Groups driving the Bank Groupings. Species Group 4 (the *Elatopathes abientina*/*Nicella* sp. group) was the largest (also containing *Peysonellia* sp.), primarily defining Bank Group 3. Species Groups 2 (the *Antipathes* sp./Gorgonian G04 group) and 3 (low species abundances) were also associated with Bank Group 3. Species Group 4 (the *Elatopathes abientina*/*Nicella* sp. group) was a major contributor to Bank Group 2 (Geyer Bank). Species Group 2 (the *Antipathes* sp./Gorgonian G04 group) was the primary constituent of the on-shelf Bank Group 1, also characterized by low species richness. Most species had a comparative abundance of ≤20%. The high species richness and affinities exhibited by Bank Group 3 are likely due to continual exposure to warm, low-turbidity Caribbean water at the shelf edge. Banks inside the shelf likely vary from the others as a result of exposure to cooler winter temperatures and higher turbidity due to wind-forced inshore currents. The reasons for the unique community structure on Geyer Bank are as yet unknown. Shelf-edge banks tend to be more species rich than on-shelf banks.**

## Introduction

*General background regarding the banks of the northern Gulf of Mexico.*—Much of the continental shelf in the northern Gulf of Mexico (GOM) is characterized by flat-bottom, covered by soft sediment. There are many areas, however, that are characterized by emergent hard-bottom banks and reefs (Rezak et al., 1985). These banks may rise to within 17 m of the sea surface. Those few that have kept up with sea level rise since the Pleistocene, as a result of coral growth on their caps, include the National Oceanic and Atmospheric Administration (NOAA) Flower Garden Banks National Marine Sanctuary (FGB; 107 km south of Sabine Pass, near Port Arthur, TX). These banks are living, thriving coral reefs, possessing a diverse set of Caribbean fauna and flora, including corals, other benthic invertebrates, fish, algae, etc. (Gittings et al., 1993; Gittings, 1998; Precht et al., 2008; Johnston et al., 2015). A number of these GOM banks occur just at or beyond the edge of the continental shelf. Most of the banks, other than the FGB, are "drowned" or relic reefs or deep coral ecosystems (Lumsden et al., 2007). These banks are generally formed in association with salt domes (or salt diapirs), which occur beneath the Earth's crust. The salt in these structures is less dense than the crust and exerts buoyant pressure upward on the crust from beneath the shelf (Gross and Gross, 1995).

Salt domes often have oil and gas deposits associated with them (Gross and Gross, 1995). Since the 1940s, oil and gas exploration and production activities in the United States have extended from inshore marine waters to offshore waters (American Oil and Gas Historical Society, 2014). It is known that oil is associated with deeper offshore GOM banks at the shelf edge (Faucon, 2013). There has been a need for the United States to become more energy-independent in recent years (e.g., Roosa, 2007). Exploration and production activities can substantially disturb benthic communities (Davies and Kingston, 1992; Peterson et al., 1996). In addition, deep-sea pelagic fisheries, such as shrimp trawling and long-lining, utilize areas around these banks, which are often adjacent to preferred trawling sites (S. Bosarge, Bosarge Boats, Gulf of Mexico Marine Fisheries Council meeting, pers. comm.). These fishing activities can also be destructive to sessile epibenthic fauna and flora (Roberts and Hirshfield, 2004; Althaus et al., 2009; Harter et al., 2009). With increasing production activity in deeper waters, there is a need to understand the character of offshore mesophotic biological communities associated with potential drill sites. This will provide government agencies such as the U.S. Environmental Protection Agency and NOAA with information designed to help protect them.

*The relationship between bottom relief and species diversity.*—Relief is defined as the vertical difference in elevation between the highest and lowest points of a surface within a specified horizontal distance or in a limited area. In tropical and subtropical marine environments, the addition of hard substratum to soft-bottom habitats enhances three-dimensional relief and complexity of habitat. This complexity facilitates the settlement of larvae of regional fauna and flora and attracts vagile adults, particularly reef fish, demersal fish, and pelagic fish. This further enhances benthic community development (Thrush and Dayton, 2002; Gratwicke and Speight, 2005) and the species diversity of the sessile epibenthic community (Bostrom and Bonsdorff, 2000; Bradshaw et al., 2003) and the associated fish community. Increased habitat complexity via increased relief can enhance the creation of refuges, spawning sites, food concentration, sites for feeding, etc. (Juanes, 2007; Roberts and Sargant, 2008).

The relationship between bottom relief and these benthic community characteristics can also be important for predicting species richness of the benthos for a given bank or a site on a bank (Sammarco et al., unpubl.). Understanding the relationship between mesophotic sessile epibenthic biodiversity and benthic relief on offshore banks is important for protecting these benthic and demersal communities (see Larsen, 1977; Carpenter et al., 1981; U.S. Department of the Interior, 1990; Garcia Charton and Perez Ruzafa, 1998). Before any relationship can be defined between these two characters, however, taxonomic diversity and its patterns must be described and understood. Then biodiversity and benthic relief can be considered in concert (McArthur et al., 2010), which in turn can lead to the construction of a model by which benthic diversity can be predicted from benthic relief, if the relationships are sufficiently robust (Sammarco et al., unpubl.). The degree of relief on these banks is currently being assessed (Sammarco et. al., unpubl.).

Previous remotely operated vehicle (ROV) surveys on these banks in the northern Gulf of Mexico have documented the presence of mesophotic reef communities on hard-bottom features that serve as fish habitat and provide substrate for the growth of sessile invertebrates. This effort produced extensive data on the biodiversity of the mesophotic benthic sessile epibiota on the same banks in the region (Sammarco et al., unpubl.). Protection from oil and gas activities is currently afforded to the crests of a number of Gulf of Mexico banks in the form of "No Activity Zones" (NAZs), in which any operations, structures, or anchoring that might disturb the benthos are restricted (Minerals Management Service, 1989; Bureau of Ocean Energy Management, 2014). These areas are designated by isobaths, which vary by bank, and range from 55 to 85 m in depth for most of the banks included in this study. Many hard-bottom features fall outside of these isobaths and harbor well-developed mesophotic epibenthic communities (E. L. Hickerson, ROV surveys, pers. comm.). Physical hard-bottom features with >2.4-m relief, called "Potentially Sensitive Biological Features" (PSBFs), are also currently protected (Minerals Management Service, 2010; Bureau of Ocean Energy Management, 2011).

This study examines the ecological communities that occur outside of the NAZ on each bank. All features with a minimum relief of 0.33 m were studied, including features characterized as PSBFs. We surveyed the sessile epibenthic community on 13 offshore banks to characterize them, including any geographic trends or patterns of association they might have.

*Objectives.*—The objectives of this study were to

1. Survey 13 banks on or inside the edge of the continental shelf in the northern GOM and quantitatively assess the mesophotic, sessile, epibenthic community there;
2. Determine any significant similarities among banks, defined by their benthic community

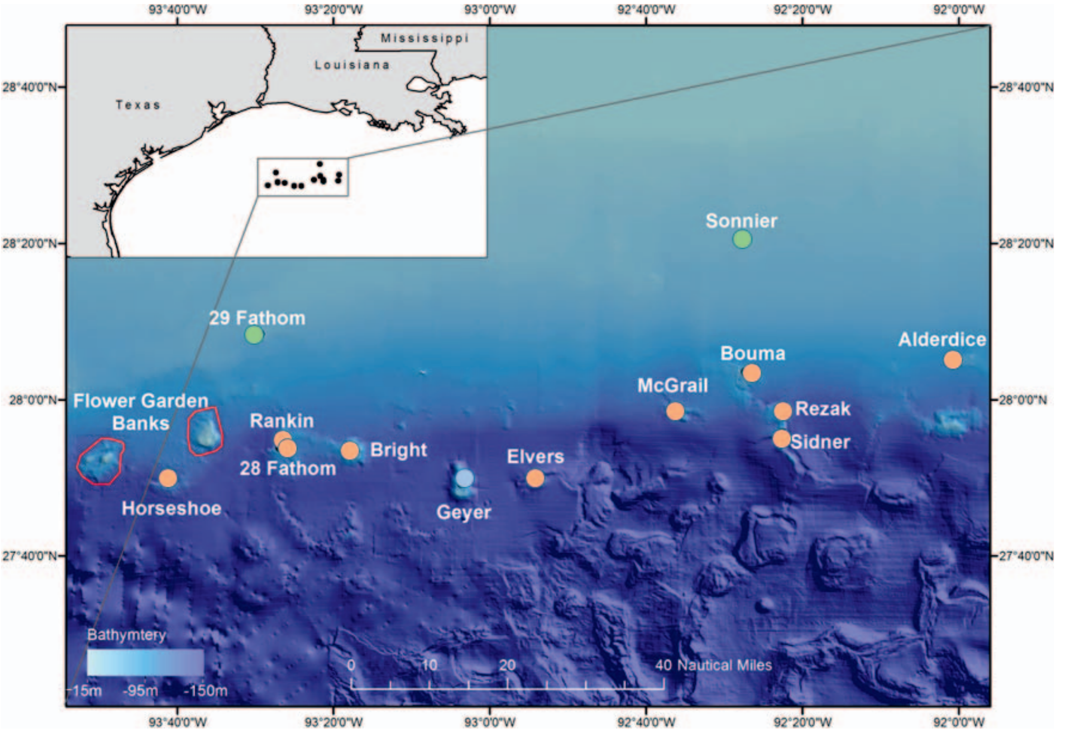


Fig. 1. Map of northern Gulf of Mexico showing the 13 offshore study banks extending from west to east, from off Port Arthur, TX, to Vermillion Bay, LA. See Table 1 for bank names. The location of the Flower Garden Banks is shown as a reference point. Each color represents a Bank Group with similar banks. The green dots represent the two northern-most banks (29 Fathom and Sonnier Banks—the on-shelf Bank Group 1). The blue dot represents one lone anomalous bank, Geyer Bank, which fell into Bank Group 2. The remainder and majority of the banks are shown in red and represent Bank Group 3, the shelf-edge group.

types, and identify how they may group together;

3. Identify those taxa and groups of taxa that are responsible for defining the above groupings of banks; and
4. Identify any geographic patterns in the distribution of the bank groupings.

## Materials and Methods

*Study sites.*—The sessile epibenthic communities were surveyed on the flanks of 13 banks in the north–central Gulf of Mexico on the continental shelf (Fig. 1). (Whole banks were not surveyed. Surveyed areas will be referred to by their bank names.) The banks extend upwards from a maximum depth of 247 m (Gardner et al., 2002). These banks occurred over a distance of 215 km from 28.338°N, −93.688°W to 27.821°N, −92.004°W. The names of the banks along with their latitudes, longitudes, and minimum and maximum sample depths may be found in Table 1. The numbers of drop-sites per bank are also shown, along with the total number of transects/bank. The deepest site/transect we surveyed was 181 m.

*Site selection.*—Areas for drop-sites for the ROV were chosen on the basis of coarse-scale (5-$m^2$ resolution), multibeam, bathymetric data (provided by the U.S. Geological Survey). Using ESRI ArcGIS, relief data were referenced for selecting sites, using the following steps: 1) In order to remove the shallower NAZ data from each bank, the bathymetry and the deeper areas outside the "core biological zones" were clipped (NOAA Flower Garden Banks National Marine Sanctuary, 2007); 2) The remaining bathymetric data were then processed using focal statistics in ESRI ArcGIS, obtaining a depth range within a 10-$m^2$ window for each cell; 3) These data were then reclassified to local relief, where 0–0.33-m height was considered flat, 0.33–2.44-m height was considered low relief, and >2.44-m height was considered high relief. The data were then converted to polygons, joined to adjacent cells

TABLE 1. List of banks in the northern Gulf of Mexico surveyed by ROV for sessile epibenthic community structure. Banks are listed in alphabetical order. Information is provided on the location (latitude, longitude) of each bank, minimum depth surveyed, maximum depth surveyed, the maximum depth of each bank (derived from www.GulfBase.org), the number of drop-sites surveyed per bank, and the total number of transects surveyed per bank.

| | | | Survey depth (m) | | | | |
|---|---|---|---|---|---|---|---|
| Bank | Latitude (N) | Longitude (W) | Minimum | Maximum | Maximum depth | Drop-sites/bank | Total No. transects/bank |
| 28 Fathom | 27.898 | −93.453 | 83.37 | 147.63 | 148 | 11 | 53 |
| 29 Fathom | 28.139 | −93.491 | 56.32 | 75.75 | 95 | 10 | 50 |
| Alderdice | 28.084 | −92.004 | 79.86 | 92.99 | 95 | 10 | 50 |
| Bouma | 28.058 | −92.454 | 84.91 | 119.71 | 120 | 10 | 45 |
| Bright | 27.892 | −93.296 | 84.87 | 132.43 | 135 | 10 | 50 |
| Elvers | 27.828 | −92.900 | 76.2 | 181.13 | 185 | 10 | 46 |
| Geyer | 27.821 | −93.061 | 85.57 | 153.79 | 190 | 10 | 50 |
| Horseshoe | 27.833 | −93.688 | 97.56 | 148.74 | 160 | 10 | 70 |
| McGrail | 27.950 | −92.565 | 86.2 | 142.87 | 145 | 10 | 50 |
| Rankin | 27.913 | −93.450 | 87.24 | 113.38 | 120 | 10 | 51 |
| Rezak | 27.969 | −92.374 | 84.72 | 120.73 | 130 | 8 | 40 |
| Sidner | 27.925 | −92.360 | 85.3 | 159.66 | 165 | 10 | 50 |
| Sonnier | 28.338 | −92.462 | 53.91 | 63.94 | 65 | 10 | 50 |

within similar relief categories, and then converted into a single unit; 4) Any polygons representing flat habitat were removed; areas of low- and high-relief polygons were included in the calculations; 5) Ten points were then randomly distributed over all habitat types, stratified by available area. A minimum interpoint distance of 100 m was used between points. These points served as our "drop-sites"—the points at which we initiated our first transect per sample point. Ten drop-sites were surveyed per bank and five random transects per drop-site, running for 10 min per transect, focusing only on hard-bottom habitats. In total, we surveyed 655 transects within 129 drop-sites on 13 banks.

*Surveys*.—Our vessel was the R/V *Manta* (NOAA Flower Garden Banks National Marine Sanctuary, Galveston, TX; National Oceanic and Atmospheric Administration, 2014c). The vessel is an aluminum-hull catamaran, water-jet propelled, with a length of 24.8 m and a beam of 9.1 m.

Benthic community data were collected on all banks in the form of high-resolution still photographs, taken vertically, using the Deep Ocean Engineering S-2 ROV (Undersea Vehicle Program, University of North Carolina, Wilmington, NC; University of North Carolina, 2014). The unit was operated by L. Horn and G. Taylor. Photographs were taken every 30 sec along a 10-min transect, resulting in ~1,000 photographs per bank. Images characterized by soft bottom or poor quality (e.g., out of focus, excessive silt, too dark) were removed. A maximum of 11 photos were then randomly selected from each transect for analysis, for a maximum of 550 photos per bank. In total, 7,150 photos were processed for sessile epibenthic community structure (e.g., Fig. 2).

The photos were analyzed at the FGB laboratories in Galveston, TX. We estimated percent-cover within each photograph for each taxon using ImageJ software. The ROV provided laser points spaced 10 cm apart, and these were transmitted onto the subject for scale. We collected percent-cover data from each photo using a 100-square grid laid over the image on the computer screen. We viewed and quantified percent-cover from images viewed using Photoshop CS5. We did not record colony size because it was not identified within the objectives of this study. We identified organisms manually to the maximum taxonomic level possible using guides developed by the NOAA-FGBNMS and partners (Hickerson et al., 2007a,b,c,d; Opresko et al., unpubl.). The research team processing these images has experience and in-depth knowledge regarding such sample processing techniques and data collection, and they have compiled reference guides for identification of the organisms encountered here. Because the ROV only had a single grab, collection of organisms was not possible except in rare cases; thus, it was only possible to identify a limited number of organisms to the species level. Data were collated using Excel and were transferred to the Louisiana Universities Marine Consortium, Chauvin, LA, and loaded onto a Dell Precision M-6600 for processing.

*Data analyses via PATN*.—PATN (Version 2.12) is a software package that conducts multivariate

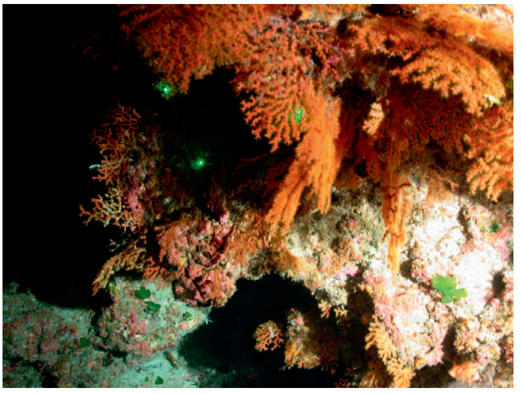

Fig. 2. An example of a still photograph generated by the Deep Ocean Engineering S-2 ROV for this study. Green points of light represent lasers set 10 cm apart directed at the subject, provided for scale. Photo taken directly vertically downward. Photos were processed manually for the purpose of assessing percent-cover of sessile epibenthic fauna and flora.

pattern-seeking analyses that extract and display patterns derived from large, complex, multivariate data sets (Belbin, 2009). It is similar to multidimensional scaling. In our case, it provided an overview of community structure trends utilizing various species abundances occurring on our study banks. Information regarding the crustose coralline algal communities was not included in these analyses but will be covered in a sister study to be published elsewhere (M. Nuttall et al., unpubl.). Our analyses were focused primarily at the bank level of resolution, incorporating all data collected and providing an overview of community structure on the banks. PATN uses its own protocols and does not mimic PRIMER. A more detailed and fine-scale analysis of these community data is being conducted by Nuttall et al. (unpubl.). It will utilize PRIMER, and the results will be complementary to the analytical results presented here. All two-way data were graphed using Sigma Plot 10.0.

PATN can be used to extract, examine, and display data patterns, generating estimates of association, which may take the form of resemblance, affinity, or distance between sets of objects. Here, our objects were banks. The sets of objects are described by a suite of variables or attributes. Here, our variables were sessile epibenthic taxa and their percent-cover. Abundances were treated as percentages. The banks were classified into Bank Groups, using the Bray–Curtis association measure (Bloom, 1981), and this classification was based upon species variables. Species Groups were generated, and these represented ecological community types.

We used an agglomerative hierarchical classification technique and opted for the "Flexible Unweighted Pair Group Method with Arithmetic Mean." This method has been used for identifying terrestrial land plant community classifications using pairwise similarities (Belbin, 2009). Species composition was used as the descriptor variable. This algorithm is used to construct a dendrogram produced using a dissimilarity matrix derived from pairwise comparisons. We then color-coded the members of the bank groupings in the dendrogram resulting from the analysis of species abundance patterns and reallocated them back to their original locations to reveal any geographic patterns in the group distributions. This analysis also produced a dissimilarity matrix of banks, based upon sessile epibenthic community structure, and provided an all-possible pairwise comparison of the 13 banks. Here, a value of 1.0 indicated complete dissimilarity, and a value of 0.0 indicated complete similarity.

*Description of PATN's delineations for species groupings.*—PATN generated a two-way table that afforded an overview of the abundance of various species occurring on each bank and their importance in driving the identification of species groupings. We used the Individual Column Standardization technique, standardizing each species entry by the maximum value within a bank. The range of abundance impact for each species was discernible in this output, varying between 0.0 and 1.0, where 1.0 represented the highest abundance of any species on a given bank. That is, the most abundant species was used as the metric against which all other species were measured for abundance. The most abundant species of, say, $n_i = 1{,}000$ would receive a ranking of 1.0, as would any other species on that bank with that abundance. A species of lower abundance on the same bank with an abundance of 500 would receive a value of 0.50, and so forth. All species abundances were thus presented as proportions. The analysis also indicated the abundance of each taxon within each bank through a color scheme (in our case, in shades of green and blue). More abundant taxa were shown in darker shades. The results fell into five categories of abundance: 0 = ≤0.2; 0.21 = ≤0.40; 0.41 = ≤0.60; 0.61 = ≤0.80; and 0.81 = ≤1.0. Absence of color in a graphic block indicates that the abundance is ≤20%.

Banks were categorized into three groups—here termed Bank Groups. The factors that drive these banks into one category or another is the number of taxa on a given bank, the species composition on that bank, and the respective species abundance. PATN also searched for suites of species that may be responsible for this

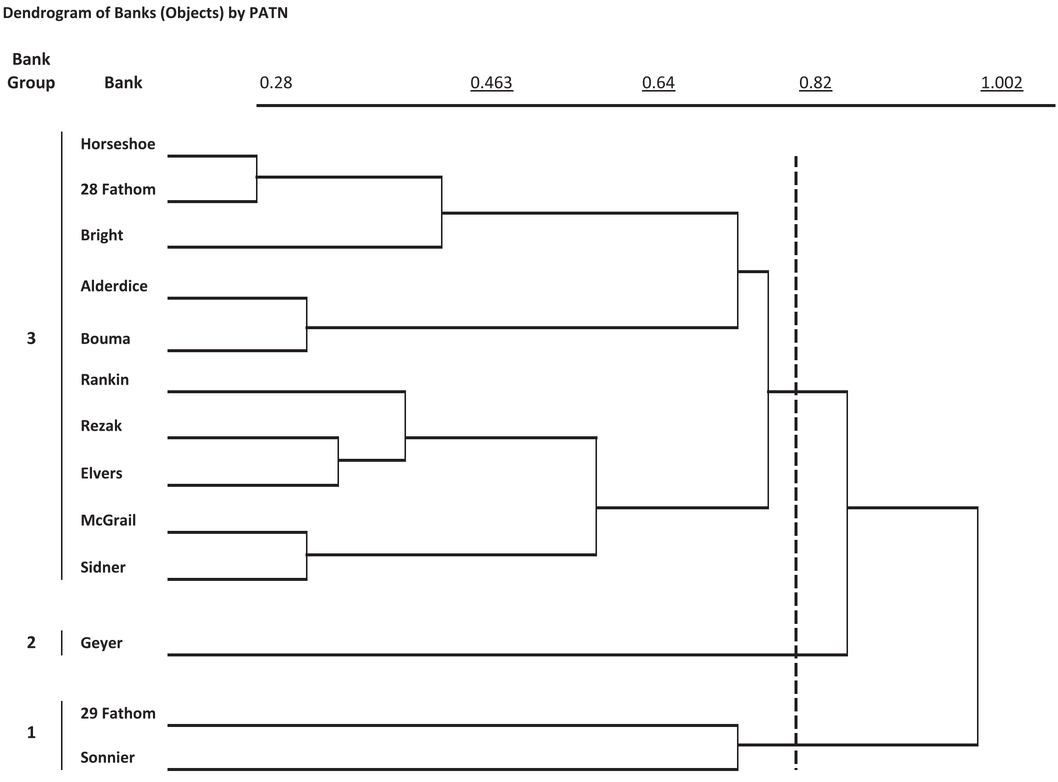


Fig. 3. Dendrogram produced by PATN, illustrating groups of banks. Bank Groupings determined by analysis of the structure of the sessile, epibenthic community on each bank. An array of dissimilarity values is shown on the top of the dendrogram. Three groups identified: the on-shelf Bank Group 1 (29 Fathom and Sonnier Banks); the anomalous Bank Group 2 (Geyer Bank); and the shelf-edge Bank Group 3 (Horseshoe, 28 Fathom, Bright, Alderdice, Bouma, Rankin, Rezak, Elvers, McGrail, and Sidner Banks).

forcing of bank categorization. It assigned those suites into groups—here termed Species Groups. In our case, four Species Groups were identified, each with its own list of species, distribution, and abundance.

*Box-and-whisker analysis.*—The box-and-whisker plots provided values for the individual Species Groups and facilitated definition of the strength of each group in making a contribution to discriminate between one Bank Group and another. The box size is a good indicator of the degree of contribution, as this denotes the inner two quartiles of the abundances in that group, 25–75%. The whiskers, on the other hand, indicate the range of the values in that species group. The individual plots extend to the right, indicating comparative abundances. The "x" associated with the box represents the mean. The scale along the top of each row represents the range of absolute abundances for that Species Group. Relative abundances are shown at the top of the table, indicating the 0%, 50%, and 100% values.

## Results

*Grouping of banks—Similarities (dendrogram and dissimilarity matrix).*—Similar banks fell into distinct groups, driven by the sessile epibenthic community on each bank (Fig. 3); this was revealed by the dendrogram produced by PATN. PATN recommends that approximately the square root of the number of objects be used for the grouping cut-off point. In this case, we had 13 banks and used three groups, conservatively rounding down. This approach resulted in 29 Fathom and Sonnier Banks being defined as a group—Bank Group 1, or the on-shelf group. Geyer Bank was identified next to be the sole member of Bank Group 2, or the anomalous shelf-edge group. The remaining banks all fell into a third group—Bank Group 3, or the shelf-edge species-rich group—Horseshoe, 28 Fathom, Bright, Alderdice, Bouma, Rankin, Elvers, McGrail, and Sidner Banks. See below for details. This last group of banks was not simply a "remainder group"; PATN perceived these banks as being more similar to each other vs the other banks using a nearest-neighbor distancing approach to analysis.

TABLE 2. Dissimilarity matrix for all banks, based upon all species of sessile epibenthic community structure. All possible pairwise comparisons shown. Data helped determine Bank Groups generated in the dendrogram shown in Figure 3. The green color associated with the bank names represents the on-shelf Bank Group 1. The red color represents the shelf-edge group—Bank Group 3. The blue color represents the anomalous bank in Bank Group 2.

| | Bank | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Bank** | **Horseshoe** | **29 Fathom** | **Rankin** | **28 Fathom** | **Bright** | **Geyer** | **Alderdice** | **Rezak** | **Bouma** | **Sonnier** | **Elvers** | **McGrail** |
| **29 Fathom** | 0.7865 | | | | | | | | | | | |
| **Rankin** | 0.6653 | 0.9019 | | | | | | | | | | |
| **28 Fathom** | 0.2835 | 0.835 | 0.6325 | | | | | | | | | |
| **Bright** | 0.4333 | 0.8106 | 0.6908 | 0.411 | | | | | | | | |
| **Geyer** | 0.7957 | 0.8631 | 0.8557 | 0.7972 | 0.6533 | | | | | | | |
| **Alderdice** | 0.6388 | 0.7755 | 0.6716 | 0.6767 | 0.7771 | 0.7853 | | | | | | |
| **Rezak** | 0.6367 | 0.9013 | 0.4253 | 0.6036 | 0.6035 | 0.7594 | 0.6256 | | | | | |
| **Bouma** | 0.5753 | 0.7548 | 0.6719 | 0.5911 | 0.7468 | 0.8137 | 0.3307 | 0.6228 | | | | |
| **Sonnier** | 0.8108 | 0.6926 | 0.8856 | 0.815 | 0.84 | 0.9024 | 0.8315 | 0.8777 | 0.76 | | | |
| **Elvers** | 0.6663 | 0.9297 | 0.3968 | 0.6411 | 0.6699 | 0.8233 | 0.7183 | 0.3334 | 0.7183 | 0.9029 | | |
| **McGrail** | 0.7052 | 0.9414 | 0.648 | 0.7215 | 0.6713 | 0.8074 | 0.7767 | 0.5048 | 0.7971 | 0.9302 | 0.5739 | |
| **Sidner** | 0.7048 | 0.9214 | 0.6437 | 0.6722 | 0.5967 | 0.6336 | 0.6787 | 0.4066 | 0.7436 | 0.9188 | 0.4997 | 0.3269 |

**0.0 = Complete Similarity**
**1.0 = Complete Dissimilarity**

The dissimilarity matrix of banks is based on the sessile epibenthic taxa and their abundances (Table 2). Therein, 0.0 designates complete similarity and 1.0 complete dissimilarity. 29 Fathom Bank was distinct, as shown by high dissimilarity values compared to those of the other banks, ranging from 0.69 to 0.94. Sonnier Bank had high dissimilarity values as well, ranging from 0.69 to 0.93. Geyer Bank, the stand-alone bank in its own group, also had high values of dissimilarity in its pairwise comparisons, ranging from 0.63 to 0.90. The remaining 10 banks had, on average, low dissimilarity indices, ranging from 0.28 to 0.88, indicating that they were more similar to each other than were the other banks.

*Geographic distribution of bank types.*—When graphed according to location, the banks within their groups revealed an interesting geographic pattern (see Fig. 1). Bank Group 3 (the shelf-edge group) banks, shown in red in the figure, occur approximately in a line, extending from the western section of the study region east–northeast to the eastern side. This trajectory tracks the edge of the continental shelf in the northern Gulf of Mexico. The anomalous lone site in Bank Group 2, Geyer Bank, occurs at the shelf edge like Elvers and the nine other banks in Bank Group 3 (the shelf-edge group), although it is very different in character than those banks.

Bank Group 1, on the other hand, shown in green, occurred further north, extending north–northeast across the study region. The banks in this group occur on the continental shelf, where the environmental conditions vary from those at the shelf edge. Here, physico-chemical factors (e.g., temperature, salinity, etc.) vary from those at the shelf edge (Hickerson et al., 2008).

*Groupings of taxa.*—The taxa encountered during this study were wide and varied, and the analysis placed them into different groups. PATN also revealed the amount of influence that each of the Species Groups had on defining the Bank Groups (Tables 3, 4). For example, all species in Species Group 1 had abundance proportions of $\leq$0.20. This included *Diodogorgia nodulifera, Thelogorgia gracilis, Plumpathes pennacea, Ventricria ventricosa,* and *Myrmikioderma gyroderma* (Supplementary Table 1, S1). We will refer to this as the *Diodogorgia nodulifera* group. (There were many unidentified species that fell into these groups.)

Species Group 2, on the other hand, comprised several species with high abundances that had significant impacts on the banks to which they were assigned (Table 3). There were several major species contributing to Species Group 2, which had a strong influence on defining several Bank Groups. Two examples of taxa possessing an abundance impact factor of 1.0 and having a major impact on assignment to given banks are *Antipathes* sp. and its influence on Sonnier Reef and Gorgonian G04 and its influence on Bouma Reef. We will refer to Species Group 2 as the *Antipathes* sp./Gorgonian G04 group. The vast majority of species, identified or unidentified, within this Species Group have less than 0.20 comparative abundances (Table S1). This includes *Muricea pendula, Higginsia coralloides, Placogorgia* sp., and *Agelas* cf. *cerebrum*. Most of the species in this Species Group were unidentified as species.

Species Group 3 contains a small number of species, and all have an abundance ranking of

TABLE 3. A two-way table generated by PATN, providing an overview of comparative abundances of sessile epibenthic species on each bank and their contributions to Species Groupings. Primary species differentiating banks are shown. Individual Column Standardization technique used to standardize each species entry within a bank by maximum value. That is, each species abundance has been standardized to a proportion, compared to the most abundant species on that bank, yielding a comparative abundance. Most abundant species driving assignment of banks to a Bank Group (0.81–1.0) are shown in large bold. Those primary species also driving bank allocations also shown in bold but in normal size font. Data analyzed using the Agglomerative Hierarchical treatment (see Fig. 3). Taxa having a major impact on assignment to Bank Groups are shown in enlarged, bold type. Comparative abundances have been color-coded using shades of green, falling into four categories: 0.21 = ≤0.40; 0.41 = ≤0.60; 0.61 = ≤0.80; and 0.81 = ≤1.0, respectively. Data for fifth category of abundance, 0 = ≤0.20, shown in Table 4.

| Species Group | | Horseshoe | 28 Fathom | Bright | Alderdice | Bouma | Rankin | Rezak | Elvers | Sidner | Geyer | 29 Fathom | Sonnier |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | All Spp. | ≤ 20%* | | | | | | | | | | | |
| 2 | Sea Frost | | | | | | | | | | | 0.4 | |
| | H13 | | | | | | | | | | | 0.4 | |
| | G12 | | | | | 0.8 | | | | | | | |
| | *Antipathes* sp. | | | | | | | | | | | | 1 |
| | DFH8-16B | | | | | | | | | | | | 0.4 |
| | SP24 | | | | | | | | | | | 0.4 | |
| | H06 | | | | | | | | | | | 0.4 | |
| | All other Spp. | ≤ 20%* | | | | | | | | | | | |
| 3 | All Spp. | ≤ 20%* | | | | | | | | | | | |
| 4 | *Elatopathes abientina* (green branching) | | 0.4 | | | | | | | | | | |
| | *Elatopathes abientina* (white branching) | 0.4 | 0.4 | | | | | | | | | | |
| | *Corallistes typus* | | 0.4 | | | | | | | | | | |
| | CR10 | | | 0.4 | | | | | | | | | |
| | *Neopetrosia* sp. | | | | | 0.4 | | | | | | | |
| | *Madrepora carolina* | | | | | 0.4 | | | | | | | |
| | Solitary Cup Coral | | | | | 0.4 | | | | | | | |
| | CR05 | | | | 0.4 | 0.4 | | | | | | | |
| | Shells | | | | 0.6 | 0.6 | | | | | | | |
| | Sea Fan | | 0.4 | 0.4 | | 0.4 | | | | | | 1 | |
| | *Acanthopathes thyoides* | | | | | 0.4 | | | | | | | |
| | *Stichopathes* sp. | | | | | 0.4 | | | | | | 0.8 | |
| | Sea Whip | | | | 0.6 | 1 | | | | | | 0.4 | |
| | *Antipathes furcata* | | | | 0.8 | 0.8 | | | | | | | |
| | *Tanacetipathes* sp. | | 0.4 | 0.4 | | 0.6 | | | | | | | |
| | Encrusting - Brown | | | | | 0.4 | 0.4 | | | | | | |
| | G04 | | | | | 0.4 | | | | | | | |
| | *Hypnogorgia* sp. | | | | 0.4 | 0.4 | | | | | | | |
| | H01 | | | | 0.4 | 0.4 | | | | | | | |
| | *Elatopathes abientina* (green) | 0.6 | 1 | 0.6 | | | | | | | | | |
| | *Elatopathes abientina* (white) | 0.6 | 1 | 0.4 | | | | | | | | | |
| | *Nicella* sp. | 1 | 1 | 0.8 | | | | | | | | | |
| | *Verdigellas* | | 0.4 | 0.4 | | | | | 0.6 | | | | |
| | Encrusting - Pink | 0.6 | 0.8 | | 0.6 | 1 | 1 | | | | | 0.4 | |
| | Encrusting - Red | 0.4 | 0.6 | | 0.4 | 1 | 1 | 0.4 | 1 | | | | |
| | Encrusting - Orange | 0.4 | 0.4 | | 0.6 | 1 | 0.6 | 0.4 | | | | 0.4 | |
| | Encrusting - Yellow | | 0.4 | | 0.4 | 0.6 | 0.4 | 0.4 | 0.4 | | | | |
| | AL12 | | 0.4 | | 1 | 0.8 | 0.6 | 1 | 1 | 1 | | | |
| | *Peysonellia* sp. | | | 1 | | | | 0.4 | 0.4 | | 1 | | |
| | Turf Algae | | | | | | | | | | 0.8 | | |
| | Hydroids | | | | 0.8 | 0.8 | | | | | | | |
| | G13 | | | | | 0.4 | | | | | | | |
| | All other Spp. | ≤ 20%* | | | | | | | | | | | |

*See Table 6

| Legend | |
|---|---|
| (light blue) | 0.4 |
| (light green) | 0.6 |
| (dark green) | 0.8 |
| (black) | 1 |

e.g., 1 = 100% abundance compared to most abundant species
0.4 = 40% abundance compared to most abundant species

TABLE 4. Collation of the most abundant five species or taxa occurring on the 13 study banks. Abundances shown. Banks presented by Bank Grouping, determined by PATN. Number of species or taxa also shown for each bank.

| | Bank group | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 3 | | | | | | | | | | 2 | 1 | |
| Species | Horseshoe | 28 Fathom | Bright | Alderdice | Bouma | Rankin | Rezak | Elvers | McGrail | Sidner | Geyer | 9 Fathom | Sonnier |
| *Nicella* sp. | 510.05 | 310.25 | 414.7 | | | | | | 570.7 | 364.4 | | | |
| *Elatopathes abientina* (white) | 256.75 | 331.45 | 229.85 | | | | | | | | | | |
| *Elatopathes abientina* (green) | 238.4 | 310.15 | 257.9 | | | | | | | | | | |
| Sponge, encrusting, pink | 227.53 | 252.2 | | | 199.2 | 1,569.85 | | | | | | | |
| Sponge, encrusting, red | 135 | 173.2 | | | 187.7 | 1,670.05 | 627.4 | 2,014.50 | | | | | |
| Sea fan | | | | | | | | | | | 180.8 | 226.75 | 108.5 |
| *Stichopathes* sp. | | | | | | | | | | | | 91.25 | |
| Sea whip | | | | 215.45 | 209.3 | | | | | | | 77.25 | |
| H13 | | | | | | | | | | | | 75 | |
| Worm, tube, bryozoan-like | | | | | | | | | | | | 71.75 | 128 |
| AL12 | | | | 362.2 | 166.4 | 780.65 | 1706 | 1,754.80 | 3,198.60 | 2,878.30 | | | |
| Sponge, encrusting, orange | | | | 188.3 | 196.3 | 684.9 | 498.3 | | | 385.2 | | | |
| Sponge, encrusting, yellow | | | | | | 507.2 | 373.8 | 424 | | | | | |
| *Peysonellia* sp. | | | 586.5 | | | | 596.2 | 428.3 | | 537.75 | 1,343.40 | | |
| *Tanacetipathes* sp. | | | 205.35 | | | | | | | | | | |
| Turf algae | | | | | | | | | | | 994.2 | | |
| Hydroids | | | | 281.4 | | | | | 635.9 | 534.25 | 560.8 | | |
| *Beggiatoa* sp. | | | | | | | | | | | 163.5 | | |
| *Antipathes furcata* | | | | 225.5 | | | | | 533.9 | | | | |
| *Antipathes* sp. | | | | | | | | | | | | | 1,216.55 |
| DFH8-16B | | | | | | | | | | | | | 305.8 |
| G04 | | | | | | | | | | | | | 116.6 |
| *Verdigellas* | | | | | | | | 909 | | | | | |
| AL04 | | | | | | | | | 498.9 | | | | |
| Total No. species and taxa per bank | 174 | 168 | 117 | 134 | 140 | 207 | 146 | 157 | 128 | 132 | 89 | 56 | 116 |

≤0.20. This is similar to Species Group 1—the *Diodogorgia nodulifera* group (Table S1). This would include *Montastraea cavernosa, Axinella waltonsmithii, Caulerpa* sp., *Plakortis zyggompha,* and *Microdictyon* sp. We will refer to this as the *Montastraea cavernosa/Axinella waltonsmithii* group. Most of the other species are yet to be identified. Here, there were no species that reached a measurable abundance impact.

Species Group 4 is the group with by far the greatest number of species and the highest comparative abundances (Table 3). This included Sea Fan and *Stichopathes* sp., helping to force 29 Fathom Reef into the on-shelf Bank Group 1. Sea whip and *Antipathes furcata,* along with the three encrusting sponges—red, pink, and orange in color—Algae AL-12 UnID, and hydroids all contributed strongly to the definition of Bouma Reef in Bank Group 3 (the shelf-edge group). *Elatopathes abientina* (white and green color morphs), *Nicella* sp., and a pink encrusting sponge contributed strongly to characterizing 28 Fathom Bank and influencing its assignment to Bank Group 3. *Antipathes furcata,* hydroids, and Algae AL-12 UnID all characterized Alderdice Bank, influencing its allocation to Bank Group 3. Algae AL-12 UnID dominated Rezak Bank as well as Elvers, McGrail, and Sidner Banks, forcing these Banks into Bank Group 3 (the shelf-edge group). A red encrusting sponge was also responsible for contributing to the assignment of Elvers Bank to Bank Group 3 (the shelf-edge group). Rankin Bank was characterized primarily by pink and red encrusting sponges, also helping to place it into Bank Group 3. Geyer Bank was unique among the different banks and was characterized by *Peysonnelia* sp. and turf algae, driving it into its own anomalous Bank Group 2. Those species with lowest comparative abundances in Species Group 4 included *Muricea* sp. cf. *furta, Aphanipathes pedata, Acanthella cubensis, Ircinia* sp., *Chironepthya caribaea,* and *Madracis* cf. *asperula* (Table S1). We shall refer to Species Group 4 as the *Elatopathes abientina/Nicella* sp. group.

If one considers only the five most abundant sessile epibenthic taxa occurring on each bank, it becomes evident that Bank Group 3 (the shelf-edge group), possessing 10 banks, was widely represented by high species abundances (Table 4). These included *Nicella* sp., *Elatopathes abientina* (two color morphs), and unidentified pink and red encrusting sponges. This set also exhibited a high level of species richness, ranging from 117 to 207 species per bank. Species composition of the five most abundant species within that group varied greatly. Horseshoe, 28 Fathom, and Bright Banks exhibited strong similarities in dominant species representation as one subgroup. The remainder of the banks in the large Bank Group 3 (the shelf-edge group) comprised a subgroup, characterized primarily by *Peysonellia* sp., yellow and orange encrusting sponges, unID algae #12, and a red encrusting sponge. 29 Fathom and Sonnier Banks—comprising the on-shelf Bank Group #1—on the other hand, exhibited overlap in comparative abundance with each other in only two of the five most abundant species within this Bank Group. These were a sea fan–shaped antipatharian and a bryozoan-like tubeworm. Both banks, however, possessed low species richness when compared to the 10 banks in Bank Group 3 (the shelf-edge group). The species richness on 29 Fathom Bank is particularly low, comprising only 56 taxa.

The dominant species on Geyer Bank included *Peysonnelia* sp., turf algae, and hydroids as its most abundant taxa. The species richness on Geyer Bank was also particularly low in comparison to that of almost all other banks, comprising the second lowest number, at 89 species.

*Influence of taxa on bank groupings (box-and-whisker results).*—Bouma Bank was well differentiated from all other banks within Bank Group 3 (the shelf-edge group), driven by the distribution and abundances of the fauna and flora in Species Group 4 (the *Elatopathes abientina/Nicella* sp. group) and also Species Group 2 (the *Antipathes* sp./Gorgonian G04 group; Fig. 4). 28 Fathom Bank mimicked this pattern to some degree. The remainder of the banks within Bank Group 3 possess very similar profiles in their Species Groups. That is, Species Group 4 (the *Elatopathes abientina/Nicella* sp. group) made the largest contribution to the characterization of this set of banks, with the additional influence of Species Group 2 (the *Antipathes* sp./Gorgonian G04 group)].

The on-shelf Bank Group 1 contains 29 Fathom and Sonnier Banks. There, Species Group 2 (the *Antipathes* sp./Gorgonian G04 group) had the strongest presence and influence on bank characterization, with a secondary influence by Species Group 4 (the *Elatopathes abientina/Nicella* sp. group). Species Group 4 had the widest range of species abundances on all banks across all Bank Groups. Geyer Bank, the stand-alone bank in the dendrogram (see above), was characterized by a low presence of Species Group 4 and almost no influence of other Species Groups. This indicates a species depauperate setting for this bank.

## Discussion

Ten out of 13 of the banks that we surveyed, or at least the flanks of these banks, were not differentiable from each other with respect to species composition and abundance. At the other end of the spectrum were 29 Fathom and Sonnier Banks, which were characterized by a different set of species. This could possibly have been influenced by light transmission, because these two banks are the shallowest of all 13. On the other hand, Geyer Bank fell between these two sets of banks as the anomalous sole representative of the anomalous Bank Group (Bank Group 2). Geyer was characterized by its low representation of flora and fauna and a unique set of abundant species. Thus, we have three major groups of banks—one large one—driven primarily by Species Group 4 (the *Elatopathes abientina/Nicella* sp. group); another single bank, driven by low biodiversity and a mild forcing by Species Group 4; and another driven by Species Group 2 (the *Antipathes* sp./ Gorgonian G04 group) and a low level of Species Group 4.

The first group of banks, Sonnier and 29 Fathom, were characterized by high dissimilarity values derived from all pairwise comparisons for assessment. This was mimicked by Geyer Bank in the second Bank Group. The remaining 10 banks all had lower dissimilarity values.

Additional insight regarding the Bank Groupings emerged when the banks and their group identities were placed into a geographic context. It became obvious that most of the banks—the 10 that fell into Bank Group 3 (the shelf-edge group)—were all located at or near the edge of the continental shelf. This region is characterized by warm, relatively clear seawater derived ultimately from the Caribbean Current (Schmitz et al., 2005). Indeed, it is one of the reasons why the FGB (near Horseshoe Bank) is able to maintain a thriving coral reef ecosystem in its shallow offshore waters, unlike some of its sister banks in the region, such as Stetson Bank. Stetson occurs 48 km NW of the FGB (GulfBase.org, 2015) and possesses scleractinian corals but has not developed as a true coral reef with a carbonaceous cap during the Holocene (Zingula, 2008, 2015). This is primarily because of its local environmental conditions, which are suboptimal for such development. The two banks in on-shelf Bank Group 1—29 Fathom and Sonnier—both occur farther north on the continental shelf, in a manner similar to Stetson Bank. There the water is cooler than on the edge of the continental shelf as a result of inshore cooling during the winter (Pulley, 1963; NOAA Flower Garden Banks National Marine Sanctuary, 2014b). The benthic fauna and flora are different there than at the shelf edge.

Geyer Bank was the stand-alone bank that falls geographically in the middle of the remaining 10 banks at the shelf edge. It was positioned at the shelf edge and, despite this, had a very low abundance and biodiversity of sessile, epibenthic fauna and flora. The reasons for this are not clear. Extensive ROV reconnaissance confirmed that the bank is characterized by *Peyssonellia* sp., a high abundance of turf algae, and hydroids. SCUBA dives by members of the research team on the cap of this reef down to 33 m have revealed that this bank could be classified as an algal ridge. Its shape is apparently the result of two salt domes merging and is characterized by a number of pinnacles (NOAA Flower Garden Banks National Marine Sanctuary, 2014a). In addition, this bank was small, and the NAZ took up a large proportion of its area, an area more limited in size to survey when compared to the other study banks. The low biodiversity of fauna and flora there caused PATN to separate it out from the other banks.

Certain species or taxa were critical in defining the Bank Groups. Considering only the most abundant species in each species group, it became obvious that the community structure was quite different between Species Groups. It also became obvious that Species Group 4 (the *Elatopathes abientina/Nicella* sp. group) was a primary driving factor in directing 10 of the banks to a single Bank Grouping. This Species Group was characterized by numerous species, many in high abundance, unlike any of the other Species Groups. Species Groups 1 (the *Diodogorgia nodulifera* group) and 3 (the *Montastraea cavernosa/ Axinella waltonsmithii* group) were consistently characterized by very low abundances of all species, although the species composition was different in each group. Species Group 2 (the *Antipathes* sp./ Gorgonian G04 group) was somewhat intermediate, with several dominant species, but it had relatively low abundances of all other species.

A collation of the five most dominant species on each bank revealed some interesting patterns. For example, the dominant species on each bank may have helped to define the Bank Groupings; ultimately, however, there were other contributing factors that also helped. These included the entire array of species present, an overlap of species between sites, and the degree of species richness on each bank.

The best-developed banks appear to be those at the edge of the continental shelf. This has also been shown for the coral communities living on oil-/gas-production platforms in the same region (Sammarco et al., 2004, 2012). The two banks in the on-shelf Bank Group 1 (29 Fathom

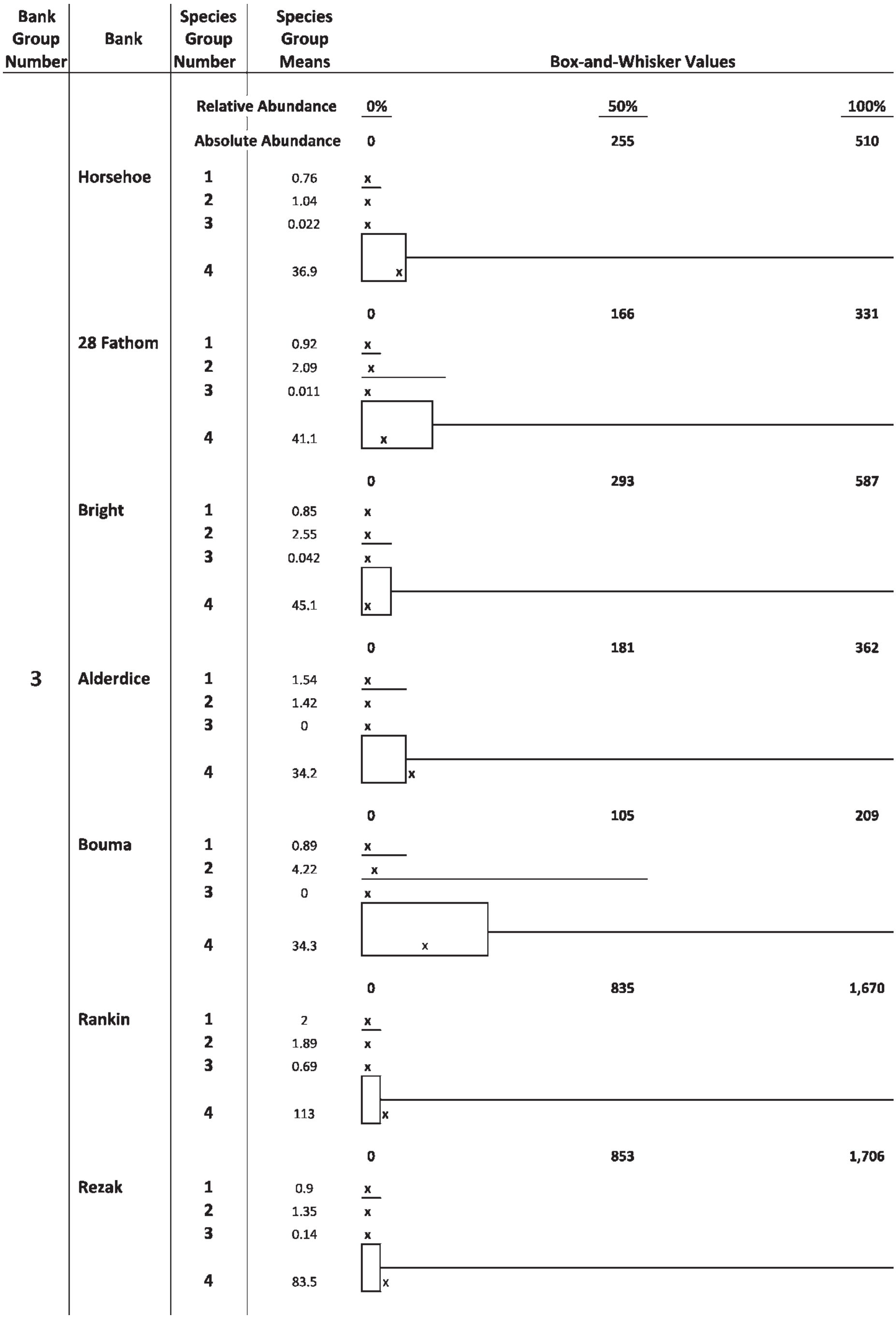


Fig. 4. Box-and-whisker diagrams (Sokal and Rohlf, 1981) showing sessile epibenthic Species Groups that best characterize a bank. The box size is an indicator of degree of contribution, denoting the inner two quartiles of the abundances in that group, 25–75%. The whiskers indicate the range of values within that species group. The individual plots extend to the right, indicating comparative abundances. For each Species Group, the far-left end of the line (or "whisker") represents the minimum value in that group; the far-right end of the line represents the maximum value for that group. The size of the box indicates major representation of that Species Group in that Bank. The "x" associated with the box represents the mean. The scale along the top of each row represents the range of abundances for that Species Group, indicating the 0%, 50%, and 100% values of the abundance.

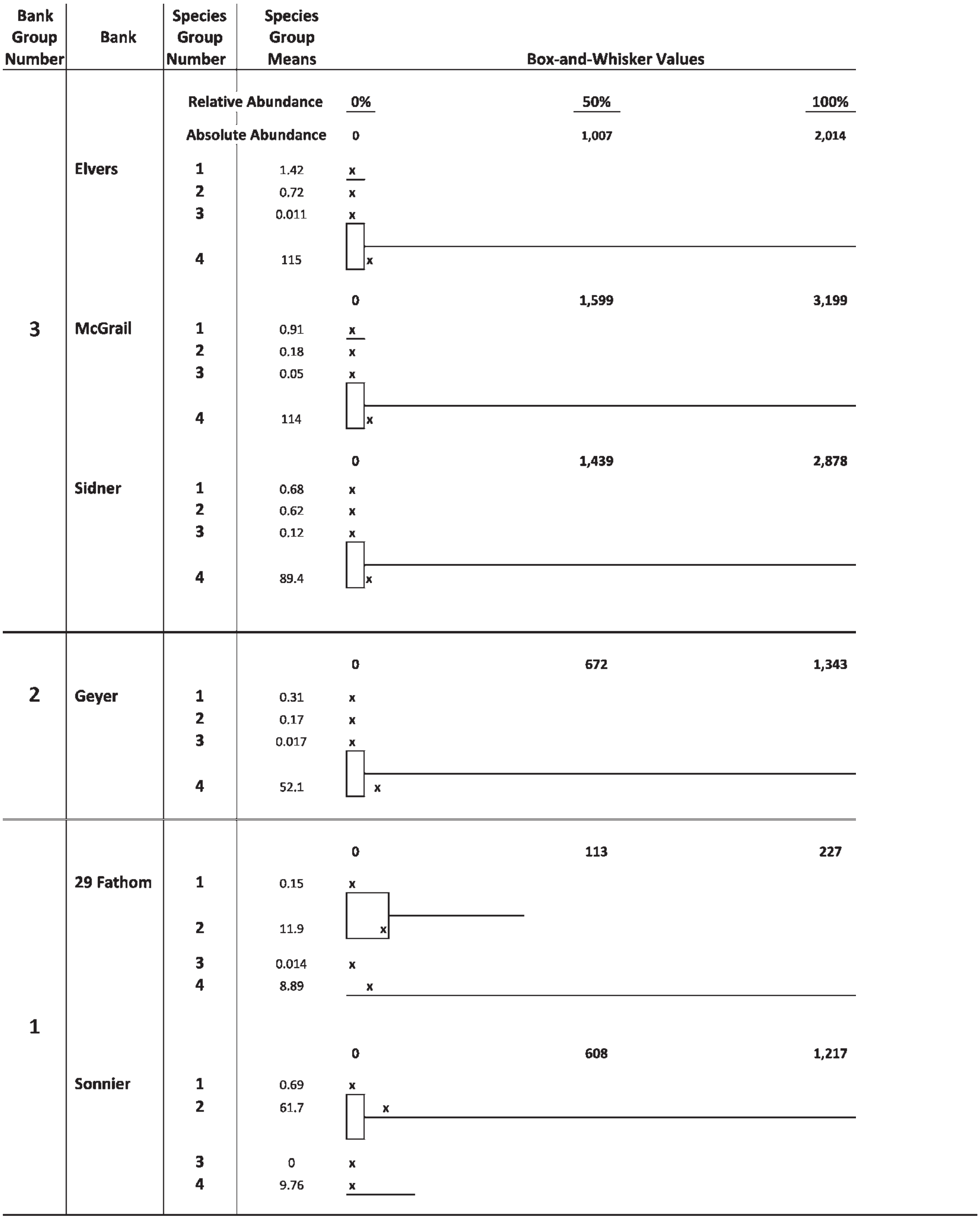


Fig. 4. Continued.

and Sonnier Banks) were quite different in their community composition from the 10 banks in Bank Group 3 (the shelf-edge group). These former banks occurred farther north on the continental shelf, closer to shore. This more northerly region is not immersed in outer-shelf edge or GOM basin water, which is generally warmer water derived from the Caribbean (Weatherly et al., 2005). We assume that these physical factors may be driving the observed differences in community composition and structure. The one bank (Geyer Bank) occurring at the edge of the shelf is poorest in biodiversity and species abundance. The reasons for this may include anthropogenic disturbance (e.g., fishing activities), disease, mortality of grazers, etc., but the actual reason(s) for the observed low diversity remains unknown at this time.

The trends resulting here regarding taxonomic diversity on these banks suggest that if benthic relief is driving benthic diversity, those banks at the shelf edge (Bank Group 3) would be expected to have the most relief and that those from the on-shelf Bank Groups 1 and the anomalous Bank Group 2 might be expected to have the lowest relief. If this were the case, one would then be able to predict, to a certain degree, the benthic species diversity from benthic relief. Now that the benthic diversity of these banks is known, it will be possible to test for this relationship. These analyses are currently underway and the results will be presented elsewhere.

In conclusion, the ROV surveys have demonstrated that most of the mesophotic, sessile, epibenthic communities on the flanks of the 13 banks surveyed, outside of the current NAZs, in this north–central Gulf of Mexico region are healthy, diverse, thriving communities, most likely qualifying as PSBFs, warranting consideration for protection. These surveys, of course, only considered hard-bottom features with any relief. It is recommended that surveys also be performed on soft-bottom features in this region on these or similar reefs. This is because they may also harbor abundant populations of benthic organisms and may also qualify as PSBFs. Such assessments should probably also include the NAZs.

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## Literature Cited

Althaus, F., A. Williams, T. A. Schlacher, R. J. Kloser, M. A. Green, B. A. Barker, N. J. Bax, P. Brodie, and M. A. Schlacher-Hoenlinger. 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Mar. Ecol. Prog. Ser. 397:279–294. doi:10.3354/meps08248

American Oil and Gas Historical Society. 2014. Offshore petroleum history: American Oil and Gas Historical Society, Washington, DC. Available from http://aoghs.org/offshore-history/offshore-oil-history/ (accessed Sep. 11, 2014).

Belbin, L. 2009. PATN, Version 3.12. Blatant Fabrications Pty. Ltd., Carlton, Tasmania, Australia. Available from http://www.patn.com.au/ (accessed on Sep. 7, 2015).

Bloom, S. A. 1981. Similarity indices in community studies: potential pitfalls. Mar. Ecol. Prog. Ser. 5:125–128.

Bostrom, C., and E. Bonsdorff. 2000. Zoobenthic community establishment and habitat complexity—the importance of seagrass shoot-density, morphology, and physical disturbance for faunal recruitment. Mar. Ecol. Prog. Ser. 205:123–138.

Bradshaw, C., P. Collins, and A. R. Brand. 2003. To what extent does upright sessile epifauna affect benthic biodiversity and community composition? Mar. Biol. 143:783–791.

Bureau of Ocean Energy Management. 2011. Deep-water Potentially Sensitive Biological Features (PSBF's) surrounding shelf-edge topographic banks in the northern Gulf of Mexico (GM-11-01a). U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), New Orleans, LA. Available from http://www.boem.gov/GM-11-01a/ (accessed Sep. 18, 2015).

———. 2014. Leasing activities information: Western and central Gulf of Mexico topographic features stipulation map package for oil and gas leases in the Gulf of Mexico. Bureau of Ocean Energy Management, New Orleans, LA. 39 p.

Carpenter, K. E., R. I. Miclat, V. D. Albaladeio, and V. T. Cornuz. 1981. The influence of substrate structure on the abundance and diversity of Philippine reef fish. Proc. 4th Int. Coral Reef Symp., Manila 2: 497–502.

Davies, J. M., and P. F. Kingston. 1992. Sources of environmental disturbance associated with offshore oil and gas developments. IAEA/INIS 24(3). Available from https://inis.iaea.org/search/search.aspx?orig_q=RN:24010707 (accessed Oct. 9, 2015).

FAUCON, B. 2013. Oil companies go deep. Wall Street Journal, Nov. 11, 2013, Available from http://online.wsj.com/news/articles/SB10001424052702303442004579123560225082786 (accessed Sep. 12, 2014).

GARCIA CHARTON, J. A., AND A. PEREZ RUZAFA. 1998. Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. Mar. Ecol. 19:111–128. doi:10.1111/j.1439-0485.1998.tb00457.x

GARDNER, J. V., J. D. BEAUDOIN, J. E. HUGHES CLARKE, AND P. DARTNELL. 2002. Multi-beam mapping of selected areas of the outer continental shelf, northwestern Gulf of Mexico: data, images, and GIS. U.S. Geological Survey, Washington, DC. Open-File Report 02-411. Available from http://pubs.usgs.gov/of/2002/0411/ (accessed Aug. 25, 2015).

GITTINGS, S. R. 1998. Reef community stability on the Flower Garden Banks, Northwest Gulf of Mexico. Gulf Mex. Sci. 16:161–169.

———, G. S. BOLAND, K. J. P. DESLARZES, D. K. HAGMAN, AND B. S. HOLLAND. 1993. Long-term monitoring of the East and West Flower Garden Banks, Final Report. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico, OCS Regional Office, New Orleans, LA, OCS Study MMS 92-0006.

GRATWICKE, B., AND M. R. SPEIGHT. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats: J. Fish Biol. 66:650–667. doi:10.1111/j.0022-1112.2005.00629.x

GROSS, G., AND E. GROSS. 1995. Oceanography: a view of the Earth. Prentice-Hall Publishers, Upper Saddle River, NJ. 472 p.

GULFBASE.ORG. 2015. Stetson Bank. *In:* GulfBase: Resource Database for Gulf of Mexico Research. Moretzsohn, F., J. A. Sánchez Chávez, and J. W. Tunnell, Jr. (eds.), World Wide Web electronic publication. Available from http://www.gulfBase.org/reef/view.php?rid=‴stetson (accessed Sep. 28, 2015).

HARTER, S. L., M. M. RIBERA, A. N. SHEPARD, AND J. K. REED. 2009. Assessment of fish populations and habitat on Oculina Bank, a deep-sea coral marine protected area off eastern Florida. Fish. Bull. 107: 195–206.

HICKERSON, E., G. P. SCHMAHL, AND M. ROBBART. 2008. The state of coral reef ecosystems of the Flower Garden Banks, Stetson Bank, and other banks in the northwestern Gulf of Mexico. National Ocean Service, National Oceanic and Atmospheric Administration, Silver Spring, MD. Available from http://ccma.nos.noaa.gov/ecosystems/coralreef/coral2008/pdf/fgbnms.pdf (accessed Sep. 18, 2015).

HICKERSON, E. L., G. P. SCHMAHL, K. BYERS, D. C. WEAVER, P. ETNOYER, G. WILLIAMS, S. CAIRNS, T. BAYER. M. K. WICKSTEN, AND L. HORN. 2007a. Octocorals of deepwater communities in the northwestern Gulf of Mexico. NOAA Flower Gardens Bank National Marine Sanctuary, Galveston, TX. [Poster.]

———, ———, ———, ———, L. HORN, K. RUETZLER, AND C. SAVARESE. 2007b. Sponges of deepwater communities in the northwestern Gulf of Mexico. NOAA Flower Gardens Bank National Marine Sanctuary, Galveston, TX. [Poster.]

———, ———, D. M. OPRESKO, M. WICKSTEN, D. WEAVER, K. BYERS, S. CAIRNS, AND L. HORN. 2007c. Antipatharians of deepwater communities in the northwestern Gulf of Mexico. NOAA Flower Gardens Bank National Marine Sanctuary, Galveston, TX. [Poster.]

———, ———, M. K. WICKSTEN, D. C. WEAVER, K. BYERS, L. HORN, S. FREDERICQ, S. CAIRNS, C. POMORY, C. MESSING, G. HENDLER, W. TUNNELL, F. MORETZSOHN, AND J. FORSYTHE. 2007d. Algae and invertebrates of deepwater communities in the northwestern Gulf of Mexico. NOAA Flower Gardens Bank National Marine Sanctuary, Galveston, TX. [Poster.]

JOHNSTON, M. A., M. F. NUTTALL, R. J. ECKERT, J. A. EMBESI, N. C. SLOWEY, E. L. HICKERSON, AND G. P. SCHMAHL. 2015. Long-term monitoring at the East and West Flower Garden Banks National Marine Sanctuary, 2011–2012: Vol. 1: Technical Report. U.S. Department of the Interior, Bureau of Ocean Energy Management, Gulf of Mexico OCS Region, New Orleans, LA, OCS Study BOEM 2015-0194.

JUANES, F. 2007. Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. J. Fish Biol. 70:661–677. doi:10.1111/j.1095-8649.2007.01394.x

LARSEN, L.-H. 1977. Soft-bottom macro invertebrate fauna of North Norwegian coastal waters with particular reference to sill-basins. Part one: bottom topography and species diversity. Hydrobiology 355:101–113.

LUMSDEN, S. E., T. F. HOURIGAN, A. W. BRUCKNER, AND G. DORR (EDS.). 2007. The state of deep coral ecosystems of the United States. Technical Memorandum CRCP-3, National Oceanic and Atmospheric Administration (NOAA), Silver Spring, MD. Available from http://www.coris.noaa.gov/activities/deepcoral_rpt/

MCARTHUR, M. A., B. P. BROOKE, R. PRZESLAWAKI, D. A. RYAN, V. L. LUCIEER, S. NICOL, A. W. MCCALLUM, C. MELLIN, I. D. CRESSWELL, AND L. C. RADKE. 2010. A review of surrogates for marine benthic biodiversity. GeoScience Australia 42, No. 2009/42, 61 p. Available from http://www.ga.gov.au/image_cache/GA16755.pdf (accessed Sep. 12, 2014).

MINERALS MANAGEMENT SERVICE. 1989. Environmental Impact Statement for proposed central Gulf of Mexico OCS lease sale 123 (March 1990) and proposed western Gulf of Mexico OCS lease sale 125 (August 1990). U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.

———. 2010. Notice to lessees and operators of federal oil, gas, and sulphur leases and pipeline right-of-way holders, outer continental shelf, Gulf of Mexico OCS region. U.S. Department of the Interior, Minerals Management Service, New Orleans, LA, NTL No. 2009-G39, 22 p. Available from http://www.boem.gov/Regulations/Notices-To-Lessees/2009/09-G39.aspx (accessed Oct. 20, 2015).

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA) FLOWER GARDEN BANKS NATIONAL MARINE SANCTUARY. 2007. Sanctuary Advisory Council boundary expansion recommendation. NOAA Flower Garden Banks National Marine Sanctuary, Galveston, TX, 35 p. Available from http://flowergarden.noaa.gov/

document_library/mgmtdocs/fgbboundaryrecommend.pdf (accessed Sep. 12, 2014).
———. 2014a. About your sanctuary—Geyer Bank. Available from http://flowergarden.noaa.gov/about/geyerbank.html (accessed Sep. 28, 2015).
———. 2014b. About your sanctuary—natural setting. NOAA Flower Garden Banks National Marine Sanctuary, Galveston, TX. Available from http://flowergarden.noaa.gov/about/naturalsetting.html (accessed on Sep. 28, 2015).
———. 2014c. Research Vessel R/V *Manta*. National Oceanic and Atmospheric Administration (NOAA), Flower Garden Banks National Marine Sanctuary, Galveston, TX. Available from http://flowergarden.noaa.gov/about/rvmanta.html (accessed on Sep. 18, 2015).
PETERSON, C. H., M. C. KENNICUTT II, R. H. GREEN, P. MONTAGNA, D. HARPER JR., E. N. POWELL, AND P. F. ROSCIGNO. 1996. Ecological consequences of environmental perturbations associated with offshore hydrocarbon production: a perspective on long-term exposures in the Gulf of Mexico. Can. J. Fish. Aquat. Sci. 53:2637–2654. doi:10.1139/f96-220
PRECHT, W. F., R. ARONSON, K. J. P. DESLARZES, M. L. ROBBART, D. J. EVANS, B. ZIMMER, AND L. DUNCAN. 2008. Long-term monitoring at the East and West Flower Garden Banks, 2004–2005—Interim Report, Vol. 1, Technical Report OCS Study 2008-027, U.S. Department of the Interior, Minerals Management Service, Outer Continental Shelf Branch, New Orleans, LA.
PULLEY, T. E. 1963. Texas to the tropics. Houston Geol. Soc. Bull. 6:13–19. Available from http://archives.datapages.com/data/HGS/vol06/no04/13.htm (accessed Sep. 28, 2015).
REZAK, R., T. J. BRIGHT, AND D. W. MCGRAIL. 1985. Reefs and banks of the northwestern Gulf of Mexico. John Wiley and Sons, New York. 259 p.
ROBERTS, C. M., AND H. SARGANT. 2008. Fishery benefits of fully protected marine reserves: why habitat and behavior are important. Nat. Resource Model 15:487–507. Available from http://onlinelibrary.wiley.com/doi/10.1111/j.1939-7445.2002.tb00099.x/references (accessed Aug. 25, 2015).
ROBERTS, S., AND M. HIRSHFIELD. 2004. Deep-sea corals: out of sight, but no longer out of mind. Front. Ecol. Environ. 2:123–130. Available from http://dx.doi.org/10.1890/1540-9295(2004)002[0123:DCOOSB]2.0.CO;2
ROOSA, S. A. 2007. Energy policy and sustainability in sunbelt cities in the United States. Int. J. Green Energy 4:173–196. doi:10.1080/01971520600873327
SAMMARCO, P. W., A. ATCHISON, AND G. S. BOLAND. 2004. Expansion of coral communities within the northern Gulf of Mexico via offshore oil and gas platforms. Mar. Ecol. Prog. Ser. 280:129–143.
———, ———, ———, J. SINCLAIR, AND A. LIRETTE. 2012. Geographic expansion of hermatypic and ahermatypic corals in the Gulf of Mexico, and implications for dispersal and recruitment. J. Exp. Mar. Biol. Ecol. 436–437:36–49. Available from http://dx.doi.org/10.1016/j.jembe.2012.08.009
SCHMITZ, W. J., JR., D. C. BIGGS, A. LUGO-FERNANDEZ, L.-Y. OEY, AND W. STURGES. 2005. A synopsis of the circulation in the Gulf of Mexico and on its continental margins, p. 11–30. *In:* Circulation in the Gulf of Mexico: observations and models. W. Sturges and A. Lugo-Fernandez (eds.). American Geophysical Union, Washington, DC.
SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W.H. Freeman and Co., San Francisco. 859 p.
THRUSH, S. F., AND P. K. DAYTON. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Ann. Rev. Ecol. Syst. 33:449–473.
UNIV. OF NORTH CAROLINA. 2014. Underseas vehicle program. Univ. of North Carolina at Wilmington, Wilmington, NC. Available from http://uncw.edu/uvp/(accessed Sep. 18, 2015).
U.S. DEPARTMENT OF THE INTERIOR, MINERALS MANAGEMENT SERVICE. 1990. Proceedings: Gulf of Mexico environmental studies meeting, April 4, 1990. Prepared by Geo-Marine, Inc., OCS Study/MMS No. 90-0052. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans, LA. 56 p.
WEATHERLY, G. L., N. WIENDERS, AND A. ROMANOU. 2005. Intermediate-depth circulation in the Gulf of Mexico estimated from direct measurements, p. 315–324. *In:* Circulation in the Gulf of Mexico: observations and models. W. Sturges and A. Lugo-Fernandez (eds.). American Geophysical Union, Washington, DC.
ZINGULA, R. 2008. Geology and paleontology of Stetson Bank. Available from http://flowergarden.noaa.gov/document_library/aboutdocs/geopaleostetson.html (accessed Sep. 28, 2015).
———. 2015. Geology of Stetson Bank. Available from http://flowergarden.noaa.gov/document_library/aboutdocs/geology_stetson.html (accessed Sep. 28, 2015).

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