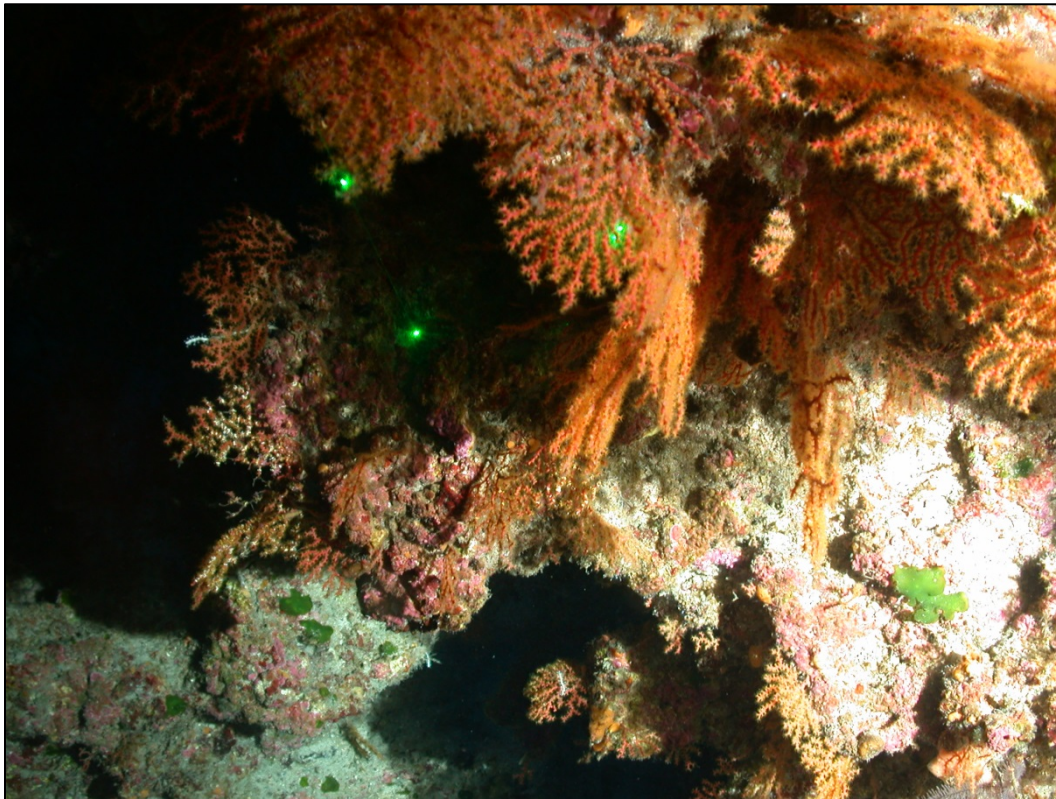


Deepwater Reconnaissance of Potentially Sensitive Biological Features Surrounding Shelf-Edge Topographical Banks in the Northern Gulf of Mexico



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ABBREVIATIONS and ACRONYMS

ArcGIS™	Arc geographical information system by Environmental Systems Research Institute (Esri)
ANOVA	Analysis of variance
BIOMStat®	Commercial statistical software by Exeter Software
BOEM	US Department of the Interior, Bureau of Ocean Energy Management
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
FGB	Flower Garden Banks National Marine Sanctuary
Gulf	Gulf of Mexico
IUCN	International Union for the Conservation of Nature
km	kilometer
m	meter
NAZ	No Activity Zone
PATN©	Commercial statistical software, incorporating a pattern-seeking analysis, by Blatant Fabrication Pty Ltd.
PSBF	Potentially Sensitive Biological Feature
ROV	Remotely-operated vehicle
SigmaPlot™	Commercial graphing software by Systat Software
Standard Deviation	SD
Standard Deviation of relief	SDR
SURFER®	Commercial three-dimensional graphics software, by Golden Software

1. INTRODUCTION

1.1 Purpose

The purpose of this study was to provide information to evaluate the quality and sensitivity of Potentially Sensitive Biological Features (PSBF) or habitats. Variability in physical relief on banks of the northern Gulf of Mexico (Gulf) may well be associated with variation in benthic biodiversity. If this is the case, and if the two factors are significantly correlated, this could provide valuable information to the oil and gas industry regarding where or where not to drill based upon geomorphological data alone. Such would provide both substantial time- and cost-savings. This study is broken into three parts: a description of relief on the target banks, a description of sessile epibenthic community characteristics, including species richness, and a correlation of the two. Each of these is covered below.

1.2 Comparative Relief on Mesophotic Reefs and Banks in the North-Central Gulf, and Their Geographic Patterns

1.2.1 General Background

The Gulf is an ancient, deep, ocean basin, with a maximum depth of ~4,000 m (13,200 ft) (Darnell and Defenbaugh, 1990; Gore, 1992). The northern Gulf has a wide continental shelf, which is generally covered by sediment of varying types (Rezak et al., 1985). This region possesses a large number of submerged banks at or near the edge of the continental shelf (Rezak et al., 1985).

These banks are generally formed in association with salt domes (or salt diapirs) underlying sediment accumulated since the salt was deposited around 200-145 million years ago during the Jurassic age. 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). Other banks are composed of bare bedrock of Tertiary or Cretaceous origin (Rezak et al., 1985). Still others are characterized by calcareous encrusting organisms, such as corals and coralline algae, and may be living reefs, or drowned or relic reefs (Bathurst, 1975; Bright and Rezak, 1976, 1978; LeBlanc et al., 1981; Rezak, 1982). The South Texas banks are built on relic carbonate substrate; the mid-shelf and shelf-edge banks are generally built above salt diapirs. Roberts (1992) asserts that the emergence of some other banks in the Gulf were influenced by the initial formation of hard-grounds by deposition of seep-related carbonates resulting from faulting, and fluid and gas migration from the deep subsurface. They then may have been raised, serving as substratum for a biologic veneer of calcium carbonate-secreting organisms. Classification of banks has been based on position on the shelf, total relief of the bank, and adjacent water depth. Location is a key factor in determining the range of seawater temperatures to bank associated communities experience. Since the Pleistocene, a few banks were able to keep up with sea level rise due to the accretion of reefal substrates as a result of growth of corals and other calcareous organisms. Examples include the Flower Garden Banks, which occur 175 km SE of Galveston, Texas. These banks possess a highly diverse set of Caribbean fauna and flora, including corals, other benthic invertebrates, fish, algae, etc. (Gittings 1992, 1998; Precht et al., 2008).

1.2.2 Importance of Hard Bottom

The purpose of this study was to provide information to evaluate the quality and sensitivity of Potentially Sensitive Biological Features (PSBF) or habitats on hard bottom. Soft bottom habitats were not surveyed due to BOEM's guidelines for this study. In tropical and sub-tropical marine environments, the addition of hard-bottom to soft bottom or featureless habitats through the growth of hermatypic corals, ahermatypic corals, gorgonians, antipatharians, sponges, and the like enhances habitat complexity. This, in turn, provides food and refuge or habitat for regional fauna and flora. It has been demonstrated that an increase in this type of habitat complexity increases populations of reef fish, demersal fish, etc. (e.g., three common gobiid species: *Coryphopterus glaucofrantum* Gill, *Gnatholepis thomsoni* Jordan, and *C. lipernes* Bohlke and Robins, Luckhurst and Luckhurst, 1978; orange roughy: *Hoplostethicus atlanticus*, Probert et al., 1977; the soft coral *Lophelia pertusa*: Thrush and Dayton, 2002; reef fish: e.g., *Abudefduf saxatilis* (L.), *Acanthurus bahianus* Castelnau, *Acanthurus chirurgus* (Bloch), *Chaetodon striatus* (L.), *Haemulon maculipinna* (Muller & Troschel), *Halichoeres radiatus* (L.), *Scarus iseri* (Bloch), *Scarus vetula* (Bloch & Schneider), *Sparisoma viride* (Bonaterre), *Thalassoma bifasciatum* (Bloch), etc., Gratwicke and Speight, 2005). Complex benthic structure as may be found in these communities can be used by these fish for refuge, spawning, concentration of food, feeding, etc. (described in detail in Juanes, 2007; Roberts and Sargent, 2008). In tropical and sub-tropical marine environments, the addition of hard substratum to soft bottom habitats enhances 3-D structure and complexity of habitat. This complexity facilitates the settlement of larvae of regional fauna and flora and attracts vagile adults, particularly reef fish and demersal fish. The benthic complexity also provides habitat for settlement of sessile benthic fauna, spawning habitat, refugia, and concentration of prey. In turn, this affects the associated fish community. Benthic habitat complexity, by providing refuge and sites for these other activities also, in turn, enhances the overall species diversity of the sessile epibenthic community, as has been found by Bostrom and Bonsdorff (2000) and Bradshaw et al. (2003).

1.2.3 Importance of Relief

There is a need to understand patterns of relief on physical structures such as offshore banks in order to understand their impact on the biological communities and their association with benthic relief. The term "relief" is used here, compared to rugosity, as would be appropriate in similar geological and geographic studies. Relief is hereby defined as "the difference between the highest and lowest elevations in an area" (About Education, Geography). We further refine this definition to include changes in elevation at the vertical spatial scale of centimeters to tens meters, within a transect or drop-site, and over a horizontal scale of meters to tens of kilometers within a bank. Comparisons of relief between banks will also be made over a scale of up to hundreds of kms. Gaining an understanding of this relationship will facilitate the protection of these benthic and demersal communities, particularly since the oil and gas industry has increased its exploration and production activities at the shelf edge and in deeper waters off the edge of the continental shelf in the Gulf. Because biological diversity can be a function of habitat complexity and the relief of these banks over a variety of spatial scales (from ms to tens of kms), it is important to describe the relief of these banks (McArthur et al., 2010). Quantifying relief could provide the needed information to construct a model by which benthic diversity can be predicted from benthic relief, if the relationship is sufficiently robust. This is not possible,

however, without first gaining an in-depth understanding of the mean relief on these banks in the mesophotic zone along with their variance.

The general degree of habitat complexity or relief on these banks has been studied by Rezak et al. (1985), although detailed information regarding relief is lacking (McArthur et al., 2010). This includes details of any patterns, particularly geographic, which these banks may exhibit in this region. Patterns in degree of relief may suggest different biological or geological processes which may have influenced feature formation. These forces could include faulting, salt diapirism causing local shoaling, and local deepening (subsequent collapse of sediment in a region due to dissolution of the underlying salt; Broecker, 1961; Rezak et al., 1985). Increased relief may also be generated by differential accretion due to the carbonate accretion activities of benthic chemosynthetic communities.

High resolution bathymetry, deep-sea submersibles, and remotely operated vehicle (ROV) explorations near shelf-edge banks in the Gulf have revealed physical variation on the seafloor associated with these banks (Rezak et al., 1985; Roberts, 1992; US Geological Survey, 2008; Roberts et al., 2010). Here, we surveyed the fine-scale topographic relief of the features surrounding several banks. There were 14 banks studied in all, and all 14 were surveyed for physical data. Only 13 banks were surveyed for biological data, due to time constraints. Parker Bank was not included in biological surveys.

Relief or rugosity (at a smaller scale) alone is not sufficient to provide valuable information which might help identify drilling sites or sites to be avoided for drilling. On the other hand, characterization of the habitat may be used as a predictor of the presence of communities or constituent species that are sensitive to potential impacts from oil and gas related activities may well be useful. In this study, the characteristics of physical relief of the PSBFs around a bank and the associated biological communities will be merged to determine whether there is a correlation between the two that may provide information to oil and gas companies and regulating agencies, such as BOEM.

1.2.4 Overall Objectives

The overall objectives of this study were to

Physical Aspects

- . Document the physical character of shelf-edge PSBFs.

Biological Aspects

- . Characterize the biological communities of shelf-edge PSBFs;
 - Determine the species occurrence, dominant species, abundance, percent-live cover, distribution, and diversity of sessile epibenthos within the study sites;
 - Conduct statistical comparisons of species occurrence, dominant species, abundance, percent live cover, distribution, and diversity of sessile epibenthos;
- . Log and identify any new species or extended distributions that occur on these PSBFs, particularly rare, threatened, endangered, endemic, or protected species.

Relationship between Physical and Biological Factors

- . Correlate various population and community variables with topographic data to determine whether the relationship between the two can be used for the purposes of providing information on potential biological sensitivity of sites with similar features; and
- . Initiate development of habitat characterization maps for PSBFs in the shelf-edge region.

1.2.4.1 Sub-Objectives - Physical Factors

With respect to the overall objective above relating to physical factors, our specific objectives were, for this section to -

- . Survey 14 banks at the edge of the continental shelf in the northern Gulf using an ROV with depth sensors and describe their comparative relief;
- . Describe their relief at three levels of spatial resolution – between banks, between drop-sites within banks, and between transects within drop-sites.
- . Determine whether there are any geographic patterns in the bottom relief of these banks over the study area.

1.2.4.2 Sub-Objectives: Biological Aspects

With respect to the above overall objectives relating to the biological aspects of the study, our specific objectives were to –

- . Survey 13 of the 14 study banks at or near the edge of the continental shelf in the northern Gulf and quantitatively assess the mesophotic, sessile, epibenthic community there;
- . Determine significant groupings of banks, defined by their benthic community types.
- . Identify those species and groups of species which are most responsible for defining those bank groupings, and
- . Identify any geographic patterns in the distribution of the bank groupings.

1.2.4.3 Sub-Objectives: Relationship between Physical and Biological Factors

Relevant to overall objectives relating to both physical and biological factors, the specific sub-objectives here were to –

- . Examine the relief data within the mesophotic zone for 13 of the banks surveyed in the north-central Gulf , using two metrics: mean and standard deviation of relief (SDR), and compare them to biodiversity data for the sessile epibenthic biota in the same zone;
- . To examine both relief and species richness simultaneously in relation to their geographic distribution and determine whether any geographic pattern exists between the two variables within the study area.

1.3 Patterns of Mesophotic Benthic Community Structure on Banks at, compared to inside, the Continental Shelf Edge

1.3.1 General Background

Much of the continental shelf in the northern Gulf 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. A few banks have kept up with sea level rise since the Pleistocene due to coral growth on their caps. The Flower Garden Banks (FGB), which occur 107 km S of Sabine Pass, near Port Arthur, Texas are an example of this. 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 mesophotic coral ecosystems, as defined by Lumsden et al. (2007) and NOAA (2011). Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and associated communities found at water depths where light penetration is low. “The term mesophotic literally translates to 'meso' for middle and 'photic' for light. The dominant communities providing structural habitat in the mesophotic depth zone can be made up of coral, sponge, and algal species. The fact that they contain zooxanthellae and require light distinguishes these corals from true deep-sea corals,” though their depth ranges may overlap. “Mesophotic coral ecosystems are typically found at depths ranging from 30-40 m and extending to over 150 m in tropical and subtropical regions.” (NOAA, 2011).

1.3.2 Mesophotic Communities

Previous ROV surveys have documented the presence of mesophotic reef communities on these prominences or hard-bottom features on banks of the Gulf that serve as fish habitat and provide substrate for the growth of sessile invertebrates. These efforts produced extensive data on the biodiversity of the mesophotic benthic sessile epibiota on the same banks in the region (Sammarco et al., work in progress a).

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 U.S. have extended from inshore marine waters to offshore (Am. Hist. Oil Gas Soc., 2014). The increasing need for the U.S. to become energy-independent (e.g., Roosa, 2007) has resulted in the extraction of oil associated with deeper offshore geologic features, often associated with processes commonly responsible for the development of shelf-edge banks. To date, there have been ~40,000 wells drilled on the continental shelf of the northern Gulf (Francois, 1993), and there are, at the time of writing, 2,304 production platforms operating in this region now.

1.3.3 History of Oil and Gas Production on the Continental Shelf

Understanding the relationship between mesophotic sessile epibenthic biodiversity and benthic relief on offshore banks is important if we are to protect their benthic and demersal communities (see Larsen, 1977; Carpenter et al., 1981; US Dept. Interior, 1990; Garcia Charton and Perez

Ruzafa, 1998). At present, there are many potential activities which could impact these benthic communities (Davies and Kingston, 1992; Peterson et al., 1996). Among them are exploration and extraction activities of the oil and gas industry.

The Bureau of Ocean Energy Management (BOEM; US Department of the Interior) currently protects the crests of these banks from oil and gas activities. They have designated No Activity Zones (NAZ; Minerals Management Service, 1989; Bureau of Ocean Energy Management, 2014). The NAZs depth limits are defined by isobaths, which vary from bank to bank, and range from 55-85m for our study banks. Numerous hard-bottom features, however, fall outside of these zones and harbor well-developed mesophotic epibenthic communities (E.L. Hickerson, ROV surveys). To protect these habitats, BOEM has extended its protection from oil and gas activities to cover PSBFs. (See Minerals Management Service, 2009 for a detailed description of PSBFs, related features of concern, and BOEM policy relating to them.) Here, the term “sensitive” is generally meant to include those species and communities that are susceptible to adverse impacts from oil and gas activities due to population size, distribution, life history, etc.

The biological communities outside of the NAZ were studied on each bank. In an effort to protect these habitats, BOEM extended protections from oil and gas activities to physical bottom features with > 2.4 m relief. These are referred to as PSBFs (Minerals Management Service, 2010; Bureau of Ocean Energy Management, 2011). NAZs and other protective measures have been in use for many years, and this type of mitigation has been helpful in protecting these banks and other areas. (See Minerals Management Service, 2009 for details on BOEM’s regulations regarding protection of marine habitats.) In fact, a new avoidance category pertaining to bottom features was recently created by BOEM as a result of increasing awareness that extensive areas of elevated features (with potential exposed hard bottom and associated communities, including corals) were not necessarily included within No Activity Zone boundaries. As stated above, this study was targeted to investigate these PSBFs outside of the No Activity Zones.

One of the purposes of studying PSBFs and other features on these banks is to determine the species present, associated communities, and key factors, if any, to assist in predicting the presence of habitats and communities requiring additional buffering from specific activities.

1.3.4 Disturbances to Offshore Banks

The mesophotic sessile epibenthic communities associated with these offshore banks are fragile, and protecting them while simultaneously managing access to OCS oil and gas resources is important. The relationship of bottom relief to these benthic community characteristics is also important for predicting species richness of the benthos for a given bank or a site on a bank. Long-lining or trawling for shrimp or other target species over wide areas of hard bottom in these areas can also be highly destructive to sessile epibenthic fauna and flora (Roberts and Hirshfield, 2004; Althaus et al., 2009; Harter et al., 2009).

In recent decades, oil and gas associated with deeper offshore GOM banks at the shelf edge has been identified as suitable for extraction. These activities can disturb benthic communities (Davies and Kingston, 1992; Peterson et al., 1996). With increasing production activity in this region, there is a concomitant need to understand the character of sensitive offshore mesophotic biological communities in order for BOEM to better identify potentially sensitive habitat and

communities and protect them by applying avoidances during the permitting process. In addition, deeper water fisheries, including long-lining and shrimp trawling, utilize areas around these banks (Steven Bosarge, Bosarge Boats, Gulf of Mexico Marine Fisheries Council meeting, pers. comm., June 2015). These activities can also act to disturb sessile epibenthic fauna and flora (Roberts and Hirshfield, 2004; Althaus et al., 2009; Harter et al., 2009).

There is a need to understand patterns of sessile, epibenthic biological community structure in order to understand how they may be associated with benthic relief on these offshore banks. Understanding that relationship will facilitate the protection of the associated benthic and demersal communities. Biological diversity is often associated with habitat complexity and fine-scale relief (see above). Before any relationship can be defined between these two characters, however, biodiversity characteristic and patterns must be described and understood. Then biodiversity and benthic relief can be considered in concert (McArthur et al., 2010), in turn leading to the construction of a model by which benthic diversity can be predicted from benthic relief (Sammarco et al., in press).

This study examines the biological communities that occur on the flanks of the banks, outside of the NAZ (since the NAZs are already protected) on each bank. All features with a minimum relief of 0.33 m were studied, including features characterized as PSBFs. We conducted biological surveys on the sessile epibenthic community of 13 out of the 14 offshore banks to characterize them and determine their structure, including any geographic trends or patterns of association they might have. The banks extend down to a maximum of 190 m (Table 1). The deepest site/transect we surveyed was at a depth of 181 m. The banks were chosen jointly by BOEM and the NOAA Flower Garden Banks National Marine Sanctuary, Galveston, Texas. All banks occurred at or near the edge of the continental shelf, offshore from Lake Sabine, Texas to Vermillion Bay, Louisiana.

Table 1. List of banks in the northern Gulf surveyed by ROV for relief.

All 14 banks listed here were surveyed for physical data. Only 13 banks were surveyed for biological data, due to time constraints. Parker Bank was not included in biological surveys.

Bank	Latitude	Longitude	Survey Depth (m)		Max. Depth (m)	NAZ Isobath (m)	n		Sample Points/ Bank
			Min.	Max.			Dropsites/ Bank	Transects/ Bank	
28 Fathom	27.898	-93.453	83.37	147.63	148	n/a	11	53	~15,000
29 Fathom	28.139	-93.491	56.32	75.75	95	n/a	10	50	30,460
Alderdice	28.084	-92.004	79.86	92.99	95	24	10	50	~14,500
Bouma	28.058	-92.454	84.91	119.71	120	26	10	45	~13,000
Bright	27.892	-93.296	84.87	132.43	135	26	10	50	13,978
Elvers	27.828	-92.9	76.2	181.13	185	26	10	46	~13,000
Geyer	27.821	-93.061	85.57	153.79	190	26	10	50	~14,500
Horseshoe	27.833	-93.688	97.56	148.74	160	n/a	10	70	~30,000
McGrail	27.95	-92.565	86.2	142.87	145	26	10	50	~14,500
Parker	27.95	-92.025	84.4	114.26	140	26	9	45	~13,000
Rankin	27.913	-93.45	87.24	113.38	120	26	10	51	~14,500
Rezak	27.969	-92.374	84.72	120.73	130	26	8	40	~11,500
Sidner	27.925	-92.36	85.3	159.66	165	26	10	50	15,131
Sonnier	28.338	-92.462	53.91	63.94	65	17	10	50	~14,500

1.2 Relationship between Relief and Species Richness, Including Geographic Patterns

1.4.1 Background on Banks of the Northern Gulf

Continental shelves can be wide and are usually characterized by a flat bottom covered with sediment. The continental shelf of the Gulf has such a bottom but also possesses a large number of submerged banks, both on and near the shelf edge (Rezak et al., 1985). The salt domes that generate the upward pressure responsible for distending the overlying bottom sediment layers often have oil or gas associated with them. Bare bedrock of Tertiary or Cretaceous origin can also comprise banks (Rezak et al., 1985). Still others may be characterized by calcareous encrusting organisms, such as corals and coralline algae, and may be living reefs like the Flower Garden Banks, or “drowned” or relic reefs (Bathurst, 1975; Bright and Rezak, 1976, 1978; LeBlanc et al., 1981).

Other forces can also be responsible for the formation of banks. The South Texas banks sit on relic carbonate substrate, while the mid-shelf and shelf-edge banks are known to be built on salt diapirs. Roberts (1992) claims that some banks in the Gulf initially emerged as hard grounds via

the deposition of carbonates by seep-associated chemosynthetic organisms, faulting, and fluid and gas migration from the deep subsurface, serving as substratum for accretion by calcium carbonate-secreting organisms. Different patterns in degree of relief may have resulted from faulting, salt diapirism, and local deepening (Broecker, 1961; Rezak et al., 1985). Differential accretion due to the carbonate accretion activities of benthic chemosynthetic communities may have also increased relief.

Location on the shelf can be a key factor in determining bank classification (Rezak et al., 1985). It can affect the range of several environmental parameters which organism experience, particularly water temperature, and this in turn can influence the distribution and abundance of organisms that can occur there (Roberts et al., 1982; Walker et al., 1982; Veron and Minchin, 1992). Variation in turbidity might also influence community structure. As sea level rose during the Recent (14,000-20,000 YBP), some banks were able to maintain their depth via coral growth on their caps (Rezak et al., 1985; e.g., the Flower Garden Banks). The Flower Garden Banks possess a fauna and flora, including corals, other benthic invertebrates, and fish which are generally a subset of the Caribbean biota (Gittings 1992, 1998; Precht et al., 2008).

1.4.2 Importance of Hard Bottom

In tropical and sub-tropical marine environments, the relationship between hard bottom and soft bottom or featureless habitats is critical to benthic community structure. In a predominantly soft bottom environment, moderate to high relief hard substrates enhance complexity. This can then serve as habitat for regional fauna and flora, particularly fish (Luckhurst and Luckhurst, 1978; Thrush and Dayton, 2002; Gratwicke and Speight, 2005). This new space becomes a preferred site for shelter, refuge, spawning, concentration of food, feeding, etc. (Juanes, 2007; Roberts and Sargant, 2008). In general, species diversity of the sessile epibenthic community will be enhanced as well (Bostrom and Bonsdorff, 2000; Bradshaw et al., 2003), and this can in turn increase species diversity in the associated fish community.

1.4.3 Relationship between Relief and Benthic Biodiversity

It is important that we understand the relationship between benthic relief and mesophotic sessile epibenthic biodiversity on offshore banks if we are to protect these benthic and demersal communities (see Larsen, 1977; Carpenter et al., 1981; US Dept. Interior, 1990; Garcia Charton and Perez Ruzafa, 1998). This is particularly important now, since there are major potential perturbations impacting these communities, as discussed above. Knowing whether the associated community has a high or low biodiversity can help guide responsible management decisions regarding the analysis of potential impacts and development of appropriate mitigations.

1.4.4 Disturbances to Banks in the Northern Gulf

One source of disturbance to banks in the northern Gulf is oil and gas exploration and development by those industries, particularly at the edge of the continental shelf and beyond (Energy Information Office, 2005). Drilling for oil/gas and extraction of petroleum hydrocarbons at the edge of the continental shelf, if not mitigated, may adversely impact benthic communities in the vicinity of these activities (Davies and Kingston, 1992; Peterson et al., 1996). The dominant anthropogenic activity potentially affecting these banks, however, is fishing and associated anchoring. The banks often fall within areas preferred by long-liners and trawlers.

The dragging for shrimp or other target species over wide areas of hard bottom in these areas can be highly destructive to sessile epibenthic fauna and flora (Roberts and Hirshfield, 2004; Althaus et al., 2009; Harter et al., 2009).

Because of the fragility of the mesophotic sessile epibenthic communities associated with these banks, there is an increasing need to locate and characterize them to guide regulatory and extraction activities by industry. The relationship of these community characteristics to relief is also important for predicting species richness of the benthos for a given bank or a site on a bank.

1.4.5 Quantifying Relief and Biodiversity on Offshore Banks, Including Geographic Patterns

A limited number of investigators have explored the biological diversity in these mesophotic habitats of the northern Gulf, where offshore banks are so prominent. Here, we will take data regarding two characters of these banks – benthic relief and species richness of the sessile epibenthic community, and examine the relationship between them (see McArthur et al., 2010). These data will be used to model that relationship in an attempt to predict benthic diversity using benthic relief.

Here, we define relief as “the difference between the highest and lowest elevations in an area” (About Education, 2015). We further refine this definition to include changes in elevation at the vertical spatial scale of cms to tens ms, within a transect or drop-site, and over a horizontal scale of ms to tens of kms within a bank. Comparisons of relief across the continental shelf will also be made over a scale of up to hundreds of kms. The term “relief” (compared to rugosity) is used here, as is appropriate in similar geological and geographic studies. In our case, surveys have been restricted to the flanks of the banks, generally deeper than 27 m. This is because the NAZs occur in shallower waters and are already protected by BOEM regulations. High resolution bathymetry, deep-sea submersibles, and remotely operated vehicle (ROV) explorations near shelf-edge banks in the Gulf (GOM) have revealed high relief seafloor features in areas surrounding a series of banks (Roberts, 1992; Gardner and Beaudoin, 2005; US Geological Survey, 2008; Roberts et al., 2010). They have also illuminated the degree of habitat complexity or fine-scale relief characterizing some of these banks, including some geographic patterns, as has been studied by Rezak et al. (1985). Previously, details regarding relief had been lacking (McArthur et al., 2010). Due to extensive physical surveys by ROV in the region of the north-central Gulf, however, we now have detailed quantitative physical data on the relief on flanks of the series of all 14 banks at or near the edge of the continental shelf in the mesophotic zone – at general depths of $\sim \geq 27$ m (Sammarco et al., in review a). Such information is important because we know that biological diversity can be a function of habitat complexity and the fine-scale relief of these banks (McArthur et al., 2010). In addition, previous ROV surveys have documented the presence of mesophotic reef communities on these features that serve as fish habitat, also providing substrate for the growth of sessile invertebrates, referred to as PSBFs (Nuttall et al., 2014; Wicksten et al., 2014). Since that time, extensive data have been collected on the biodiversity of the mesophotic benthic sessile epibiota on 13 of the 14 banks in the same region (Sammarco et al., work in progress a). This provides the necessary data with which to examine the relationship between benthic biodiversity and benthic relief and to determine

whether correlations between the two are significant. If so, the relationship might serve as a model by which to predict benthic biodiversity from relief.

1.5 Team Participants

Many people participated in this research program. All are listed in the Acknowledgements section. The primary participants are as follows:

- . Paul W. Sammarco (Professor, Louisiana Universities Marine Consortium, LUMCON, Chauvin, Louisiana), principal investigator, experimental designer, and cruise leader for the study.
- . Marissa F. Nuttall (National Oceanic and Atmospheric Administration, NOAA, Flower Garden Banks National Marine Sanctuary, Galveston, Texas), Field Coordinator, Taxonomic identification, Laboratory processing of field samples and photographic data, statistical analyses, co-writing.
- . Daniel Beltz (Research Assistant, Louisiana Universities Marine Consortium - LUMCON, Chauvin, Louisiana), data collation analysis, graphics, and field assistance, co-writing.
- . Emma L. Hickerson (co-Principal Investigator, National Oceanic and Atmospheric Administration, NOAA, Flower Garden Banks National Marine Sanctuary, Galveston, Texas), experimental design, field logistics, co-writing.
- . George P. Schmahl (National Oceanic and Atmospheric Administration, NOAA, Flower Garden Banks National Marine Sanctuary, Galveston, Texas), experimental design, NOAA-FGBNMS operations coordination, co-writing.
- . Lance Horn (Underwater Vehicles Program, University of North Carolina at Wilmington, Wilmington, NC), ROV Pilot, Ship-Board Logistics Supervisor, Relief Data Collation.
- . Glen Taylor (Underwater Vehicles Program, University of North Carolina at Wilmington, Wilmington, North Carolina), field assistance, ship-board ROV operations including maintenance, trouble-shooting, mobilization, and demobilization.

1.6 Duration

This study was conducted over a period of five years. Data collection occurred from 2010 to 2013. Efforts were delayed by tropical storms in 2011 and 2012. Photographic and relief data analyses were conducted in parallel. Finally, extensive statistical analyses were conducted. Various reports were prepared during the course of the study and submitted to BOEM.

2. MATERIALS AND METHODS

In order to provide a more logical flow of the information presented in this report, technical information and data related to the following aspects of the study will be presented in the following order, respectfully:

- . Relief on the banks
- . Biological community information on the banks, and
- . The relationship between relief on the banks and species richness.

2.1 Comparative Relief on Banks, Including Geographic Patterns

2.1.1 Study Sites

The fourteen banks surveyed for benthic relief at the edge of the continental shelf in the northern Gulf spanned an east-west distance of 215 km. They are listed along with their latitudes, longitudes, minimum depths sampled, maximum depths sampled, and sample size for no. drop-sites/bank, no. transects/drop-site, and no. relief data points per transect in Table 1. Their geographic locations are shown in Fig. 1. Throughout this document, for simplification purposes, we will refer to the surveyed areas by their bank names. They extend upwards from a maximum depth of 247 m (Gardner et al., 2002). These banks occurred over a west to east distance of 215 km from 28.338°N, -93.688°W to 27.821°N, -92.004°W (see Table 1). The names of the banks are, in alphabetical order, 28-Fathom, 29-Fathom, Alderdice, Bouma, Bright, Elvers, Geyer, Horseshoe, McGrail, Parker, Rankin, Rezak, Sidner, and Sonnier. These banks extended upwards from a maximum depth of 247 m (Gardner, 2002).

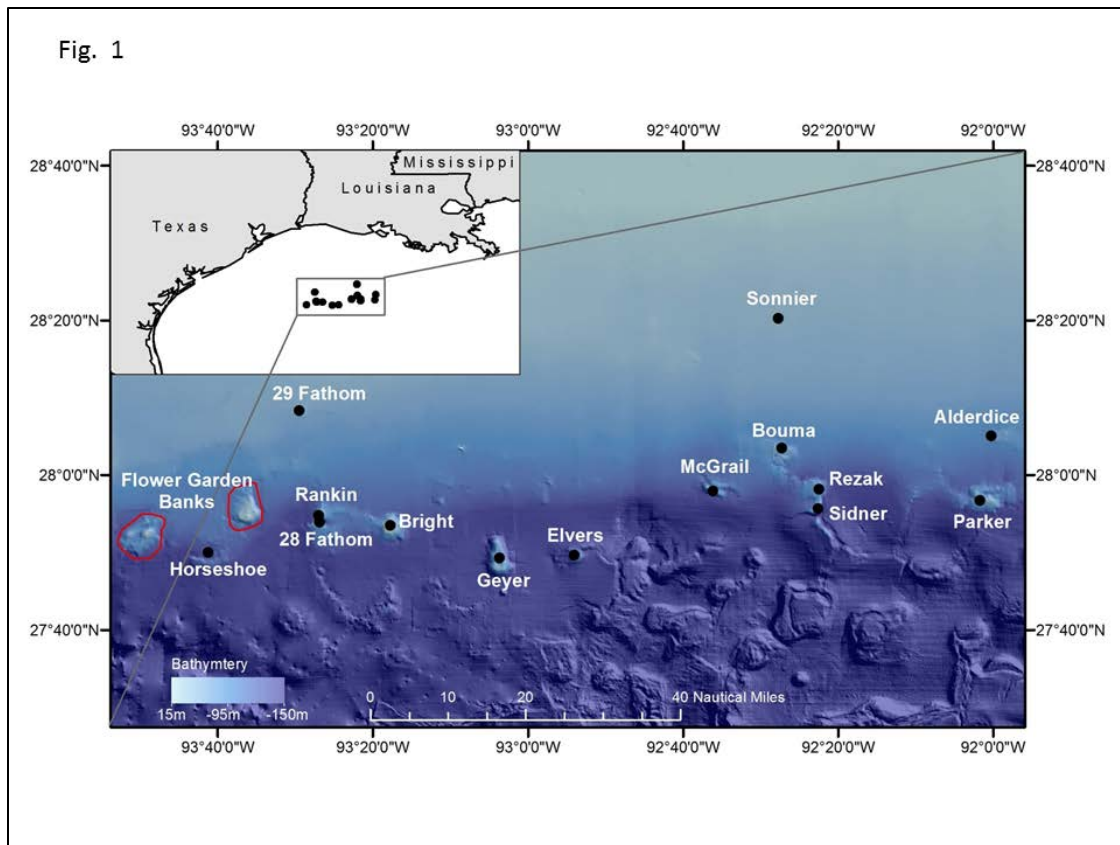


Figure 1. Map of northern Gulf indicating locations of the 14 target banks studied here.

They span from offshore Port Arthur, Texas, USA to Vermillion Bay, Louisiana and, west to east, are Horseshoe, 29 Fathom, Rankin, 28 Fathom, Bright, Geyer, Elvers, McGrail, Sonnier, Bouma, Rezak, Sidner, Parker, and Alderdice Banks. The Flower Garden Banks are shown as a reference point.

Substrate relief is a common characteristic of hard-bottom offshore banks and is associated with benthic biodiversity. Earlier studies revealed varying relief associated with offshore mesophotic communities. Establishing correlations between relief and benthic biodiversity require obtaining an estimate of variability on these banks and associated geographic patterns. We performed fine-scale surveys of the above 14 banks in the Gulf to examine variation between them, geographic patterns, and possible processes influencing their formation. We used a multi-beam sensor on an ROV, resolution = ~0.5 m. Average and standard deviation (SD) of relief were calculated in m for each transect within a sample-site, and each sample-site within each bank.

2.1.2 Surveys

Surveys were performed using the R/V *Manta* (National Oceanic and Atmospheric Administration, Flower Garden Banks National Marine Sanctuary), based in Galveston, Texas. The vessel is a water-jet propelled, aluminum-hull catamaran, 24.8 m in length, with a beam of 9.1 m.

Relief data were collected on the target banks in the form of depth measurements using the Deep Ocean Engineering S-2 ROV, owned and operated by the Undersea Vehicle Program, University of North Carolina at Wilmington, Wilmington, NC (Univ. No. Carolina Wilmington, 2014). The unit was operated on ship-board by L. Horn and G. Taylor. The ROV recorded its own depth in m (to a resolution of 0.1 m) and the distance from the vehicle to the bottom every 1–2 secs. This resulted in 300–600 points per transect, for a total of $\geq 210,000$ points for the study. The maximum depth sounded along a given transect was used as the standard against which the height of any point along that transect was calculated. Once again, each of 5 transects was 10 min. in duration, with the ROV velocity being ~ 0.3 m/sec resulting in a transect length of 180 m. The following formula was used to calculate relief:

$$Re_{ij} = D_{\max(i)} - D_{ij}$$

Where Re = Relief at given point on Transect,

i = Transect number

j = individual depth data point taken every 2 secs

D_{\max} = Maximum depth of transect i

D = Depth of individual Relief Point

Drop-sites for the ROV were chosen based upon coarser-scale (5 m resolution), multi-beam, bathymetric data on these banks, collected and provided by the US Geological Survey. These relief data were used for site selection using ESRI ArcGIS according to the following steps: 1) The bathymetry was “clipped” to remove shallower No Activity Zone (NAZ; Bureau of Ocean Energy Management) data from each bank and was also clipped to remove deeper areas outside the core biological zones, also referred to as Sensitive Habitat Zones (NOAA Flower Garden Banks National Marine Sanctuary, 2007); 2) Remaining bathymetric data were then processed using focal statistics in ERSI ArcGIS to obtain a defined depth range within a 2x2 horizontal window (representing 10 sq m); 3) These data were, in turn, re-classified to local vertical 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 and dissolved to convert these multi-part attributes to a single unit. (It should be noted that these relief designations were only used for site selection. Data collected in ROV surveys included all relief data, irrespective of height.) 4) Polygons denoting flat habitat were removed, while the area of low and high relief polygons were included in the calculations. 5) 10 points were then distributed randomly, based on area, with a min. distance of 100 m between them; these points were designated to be start locations or “drop-sites” for transects. Drop-sites were those geographic points at which the ROV was dropped over the side of the vessel to conduct its surveys. Only hard-bottom features were surveyed.

Ten drop-sites were identified for each bank and surveyed. Five transects were surveyed randomly at each drop-site. Each transect was 10 mins in duration. After each transect, the ROV stopped recording and was driven to another site where a new transect was started; i.e. transects were not contiguous. High resolution depth data were collected by the ROV every two seconds.

2.1.3 Metrics

Two indices were used to describe degree of relief on the banks. The first was a statistic of location: the arithmetic mean of relief within a transect. The second was a statistic of dispersion: the standard deviation (SD) of relief within a transect, providing information on the weighting of each point by its distance from the center of the distribution of points (Sokal and Rohlf, 1981).

2.1.4 Data Analyses

Data were analyzed via standard parametric univariate statistical analyses (Sokal and Rohlf, 1981). These included analysis of variance (ANOVA) and multiple comparisons among means. The software used to run the analyses was BIOMStat[®] (Rohlf and Slice, 1996). Details of statistical results will be presented in figure legends and also in the text. Data were graphed using SigmaPlot[®] 10.0 and Surfer[®] 8.0.

2.2 Patterns of Mesophotic Benthic Community Structure

2.2.1 Study Sites

The sessile epibenthic community was surveyed on the flanks of 13 banks in the north-central Gulf on the continental shelf. We chose areas for the drop-sites for the ROV on the basis of coarser-scale (5 m resolution) multi-beam, bathymetric data available for these banks, which were provided by the US Geological Survey. Using ESRI ArcGIS[®], these relief data were then referenced for selecting sites, using the steps described above.

As mentioned above, we identified ten drop-sites for each bank. We surveyed the bottom using five random transects per drop-site. Transects were 10 mins in duration and focused on only hard-bottom habitats, as required by BOEM.

2.2.2 Surveys

Ecological surveys were performed using the R/V *Manta*, owned and operated by the National Oceanic and Atmospheric Administration (NOAA), FGBNMS, based in Galveston, Texas, (National Oceanic and Atmospheric Administration [NOAA], 2014c).

Benthic community data were collected on the banks in the form of high-resolution still photographs, taken vertically, using the Deep Ocean Engineering S-2 ROV, owned and operated by the Undersea Vehicle Program, University of North Carolina at Wilmington, Wilmington, NC (University of North Carolina, 2014). The unit was operated on ship-board by L. Horn and G. Taylor. The same number of transects and drop-sites were sampled per bank as described above. Photographs were taken every 30 seconds along a 10-min transect. The unit recorded ~1,000 photographs per bank. Photos were processed to remove images of soft bottom or poor quality (e.g., out-of-focus, excessive silt, too dark). A maximum of 11 photos were then randomly

selected from the remainder within each transect for analysis, with a max. of 550 photos per bank). In all, 7,150 photos (max.) were processed for sessile epibenthic community structure.

The photos were analyzed at the laboratories of the FGBNMS in Galveston, Texas. The coverage of each photograph was calculated using ImageJ software, using the points appearing on the substrate from the lasers mounted on the ROV and within the view of the camera for scale. They were spaced 10 cm apart. Percent-cover data were collected from each photo using a 100-square grid laid over the image on the computer, viewing images with Photoshop® CS5. Colony counts were collected from each image. Species were identified using guides developed by the FGBNMS and partners (Hickerson et al. 2007a,b,c,d; Opresko et al., work in progress). Data were then collated using EXCEL and then transferred to the Louisiana Universities Marine Consortium in Chauvin, Louisiana and loaded onto a Dell® Precision M-6600 for further processing.

2.2.3 Data Analyses: PATN®

PATN® is a pattern-seeking analysis which analyzes large, complex multi-variate data, providing an overview of community structure trends (Belbin, 2009). In our case, it was used to analyze various species abundances occurring on our study banks. Information regarding the crustose coralline algal communities were not included in these analyses but will be discussed elsewhere (Nuttall et al., work in progress).

Sessile epibenthic community structure data were analyzed using PATN® Version 3.12. This program seeks 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 the presence of sessile, epibenthic species and their abundances. The objects or banks were then classified into Bank Groups, using the Bray-Curtis metric (Bloom, 1981) based upon the species variables. Ecological community types identified during the statistical analysis will be referred to as Species Groups.

When executing hierarchical classification, we used an agglomerative hierarchical classification technique. We also opted for using the Flexible Unweighted Pair Group Method with Arithmetic Mean. This is commonly used for identifying terrestrial land plant community classifications using pair-wise similarities (Belbin, 2009). Species composition was used as the descriptor variable. This algorithm is used to construct a dendrogram produced from pair-wise comparisons within a dissimilarity matrix. In our case, the members of the bank groupings in the dendrogram resulting from the analysis of species abundance patterns were then color-coded and re-allocated 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 the sessile epibenthic community structure. It provided an all possible pair-wise comparison of the 13 banks. In this comparison, the software generates a value of 1.0 to indicate complete dissimilarity, and 0.0 to indicate complete similarity.

2.2.4 Description of PATN[®]'s Delineations for Species Groupings

In order to provide an overview of the abundance of various species occurring on each bank and their contributions to the species groupings, PATN[®] generated a two-way table. The Agglomerative Hierarchical treatment of the data which we used assisted in the production of a dendrogram. In addition, we used the Individual Column Standardization technique, standardizing each species entry by the maximum value within the bank. The most abundant species is used as the metric against which all other species are measured for abundance. Thus, the most abundant species of, say, n=1,000 would receive a ranking of 1.0, as would any other species on that bank with that same abundance. A species of lower abundance on the same bank with an abundance of, for example, 500 would receive a value of 0.50, and so forth. All species abundances are thus presented as proportions. Identifications were made to the species level, or as close as possible to that using a still photo technique. Any lumping of species due to this analytical technique will make species richness estimates more conservative.

PATN[®] also demonstrates how abundant individual species are within each bank through a color scheme. In our case, this has been shown graphically using shades of green and blue. More abundant species are shown in darker shades. The results fell into five categories of abundance of associated benthic species:

- . 0 - \leq 0.2
- . 0.21 - \leq 0.40
- . 0.41 - \leq 0.60
- . 0.61 - \leq 0.80; and
- . 0.81 - \leq 1.0.

Absence of color in a graphic block indicates that the abundance is \leq 20%.

The analysis categorized the banks into three groups – here termed Bank Groups. The factor which drives these banks into one category or another is the number of species on a given bank, the species composition on that bank, and their respective abundances. PATN[®] also searches for suites of species which may be responsible for this forcing of bank categorization. It assigns those suites into groups, here termed Species Groups. In our case, PATN[®] identified four Species Groups, each with its own list of species, distribution, and abundance. Each Species Group was characterized by abundance of species.

2.2.5 Box-and-Whisker Analysis

After this, PATN[®] generated traditional Box-and-Whisker plots (or box plots, Sokal and Rohlf, 1981). The values for the individual Species Groups are shown and facilitate definition of the strength of each Species Group in making a contribution to discriminate between one Bank Group and another. The individual box-and-whisker plots extend to the right indicating comparative abundances. For each Species Group, the far-left end of the line represents the minimum value in that Group. The far-left end of the box represents the 25th percentile for the values in the Species Group. The far-right end of the box represents the 75th percentile. The far-right end of the line (or “whisker”) represents the maximum value of the range for that Species Group. The small circle 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.

Data were graphed using SigmaPlot[®] 10.0.

2.2.6 Habitat Characterization based on Within-Bank Distribution of Species Richness

Once the biological analysis was complete, species richness could be determined for each drop-site on each bank. Since the spatial coordinates were known for each drop-site, these data could be graphed to determine whether there was any consistent within-bank or between-bank geographic patterns to the distribution of species richness/this character. If so, this may help in habitat characterization.

2.3 Relationship between Relief and Species Richness, Including Geographic Patterns

2.3.1 Study Sites

The flanks of thirteen offshore banks were surveyed. The maximum depth in the region varied between 190 and 247 m (Gardner et al., 2002). The banks extended west to east for 215 km- from 28.139°N, -93.491°W to 28.084°N, -92.004°W.

We surveyed the sessile epibenthic community on the above 13 offshore banks and characterize both their biological and physical features, along with any geographic trends or patterns of association they might have. The deepest depth for the banks was 190 m (Table 1), and we surveyed to a maximum depth of 181 m.

The techniques by which we selected drop-sites for the banks are described above.

2.3.2 Vessel

We used the R/V *Manta* to conduct both ecological and benthic relief surveys.

2.3.3 Collection of Relief Data

As described above, relief data on the banks were collected by capturing depth measurements via a Deep Ocean Engineering S-2 ROV.

We used two indices to mathematically describe degree of relief on the banks. The first was the arithmetic mean of relief within a transect. The second was the SDR within a transect, a statistic of dispersion. This latter index provided information on the weighting of each point by its distance from the center of the distribution of points.

2.3.4 Collection of Ecological Data

We collected data on the mesophotic, sessile, epibenthic community associated with the banks by taking high-resolution still photographs, taken vertically, using the same Deep Ocean Engineering S-2 ROV, also as described above. We took photographs along a transect every 30 seconds for 10 minutes, surveying five transects per drop-site, and 10 drop-sites per bank. As mentioned above, after each transect, the ROV stopped recording and was driven to another site where a new transect was started; i.e., transects were not contiguous. Once again, the ROV velocity was ~0.12 m/sec resulting in a transect length of 36.3 m. We removed images of only soft bottom or of poor quality and then selected 11 photos (max.) from the remainder. This yielded 550 photos per bank (max.). A total of 7,150 photos were produced and processed.

Personnel at the NOAA FGBNMS in Galveston, Texas processed the photos with ImageJ[®] software. Scale was provided by parallel laser beams mounted on the ROV, spaced 10 cm apart, and appearing within the camera's view. We collected complete percent-cover data from each photo, assisted by a 100-square grid laid over the image on the computer. Colony counts were collected for antipatharians, octocorals, and scleractinians. Guides developed by the NOAA FGBNMS and its partners were used to assist in taxonomic identification (Hickerson et al. 2007a,b,c,d; Opresko et al., work in progress). Data were collated using EXCEL and relayed to the Louisiana Universities Marine Consortium, Chauvin, Louisiana for data processing on a Dell Precision M-6600.

The primary ecological variable used for this study was species richness or number of species, derived from the percent-cover data. This variable was analyzed at the bank and drop-site levels.

2.3.5 Statistics

Pearson's Product-Moment Correlation Coefficient was calculated for two-way data (Rohlf and Slice, 1996). In addition, Model II regressions were calculated. Where data were non-linear, curvilinear analyses were performed through curve-fitting analyses using Sigma Plot 10.0.

3. RESULTS

3.1 Comparative Relief on Banks, Including Geographic Patterns

3.1.1 *Overview of Relief on the 14 Study Banks*

Species richness, diversity, abundance, percent-cover, etc. are all critical characteristics which help define a benthic marine community. These species may include rare, threatened, or endangered species. All of these characteristics are known to be correlated with benthic relief (or rugosity) on a small scale – particularly on coral reefs. The relationship between these community characteristics and relief on a larger spatial scale is unknown. Here, we will define and quantify relief on this series of experimental banks to determine mean relief on each of them at several spatial scales and also the variance around that mean for each bank. Only then will it be possible to determine whether there is any relationship between relief on the banks and these community characteristics, particularly species richness (number of species).

Relief, as measured by mean height of changes in depth with respect to the bottom (deepest portion of a transect; see above), and its 95% confidence limits were calculated for each of the 14 banks. Means were calculated from data for each transect (5/drop-site) and for each drop-site within each bank (10/bank). There was a significant difference in relief between banks using mean heights ($p < 0.001$, nested ANOVA; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests) and also between drop-sites ($p < 0.001$, nested ANOVA; $p < 0.05$, multiple comparisons tests). The banks were ranked in terms of degree of relief from highest to lowest and are shown in Fig. 2a. The range of relief varied between an overall mean of 1.6 m around 29-Fathom Bank, the bank possessing the least overall relief, to 3.8 m around McGrail Bank, one of the banks possessing a high overall relief. The banks which were determined to be significantly different from each other in mean relief are shown in Table 2a.

Table 2. Multiple pair-wise comparisons in bottom relief between banks surveyed in the northern Gulf.

* = $p < 0.05$ by T', T-K, or GT2 tests. Only significant differences between banks are shown.

(A) Comparisons of relief between reefs using mean relief as an index. (B) Comparisons of relief using the SD as an index.

(A)					
Mean Relief					
Bank	Horseshoe	Rankin	Elvers	Sidner	McGrail
Sonnier	*	*	*	*	*
29-Fathom	*	*	*	*	*
Alderdice				*	*
(B)					
SDR					
Bank			Bank		
	Elvers	Sidner	Rankin	McGrail	Horseshoe
Sonnier	*	*	*	*	*
29-Fathom		*	*	*	*
Alderdice		*	*	*	*
Geyer					*
Rezak					*
Parker					*
Bright					*
Bouma					*

Relief values as measured by SD are plotted in Fig. 2b. The SDR index yielded results and trends similar to those using the mean, above. There was a significant difference between banks using the SD of heights ($p < 0.001$, nested ANOVA), and between drop-sites ($p < 0.001$). Sonnier and McGrail Banks exhibited the lowest and highest SDR, respectively, with values for all other banks falling between them. SD of relief (Fig. 2, right-hand panel) varied between 0.7 m at Sonnier Bank to 1.8 m around McGrail Bank, with the other banks yielding intermediate values. Those banks which were determined to be significantly different from each other in relief using the SD as an index are shown in Table 2b. These data demonstrate that the SD was more sensitive to differences in relief between banks than is the mean index.

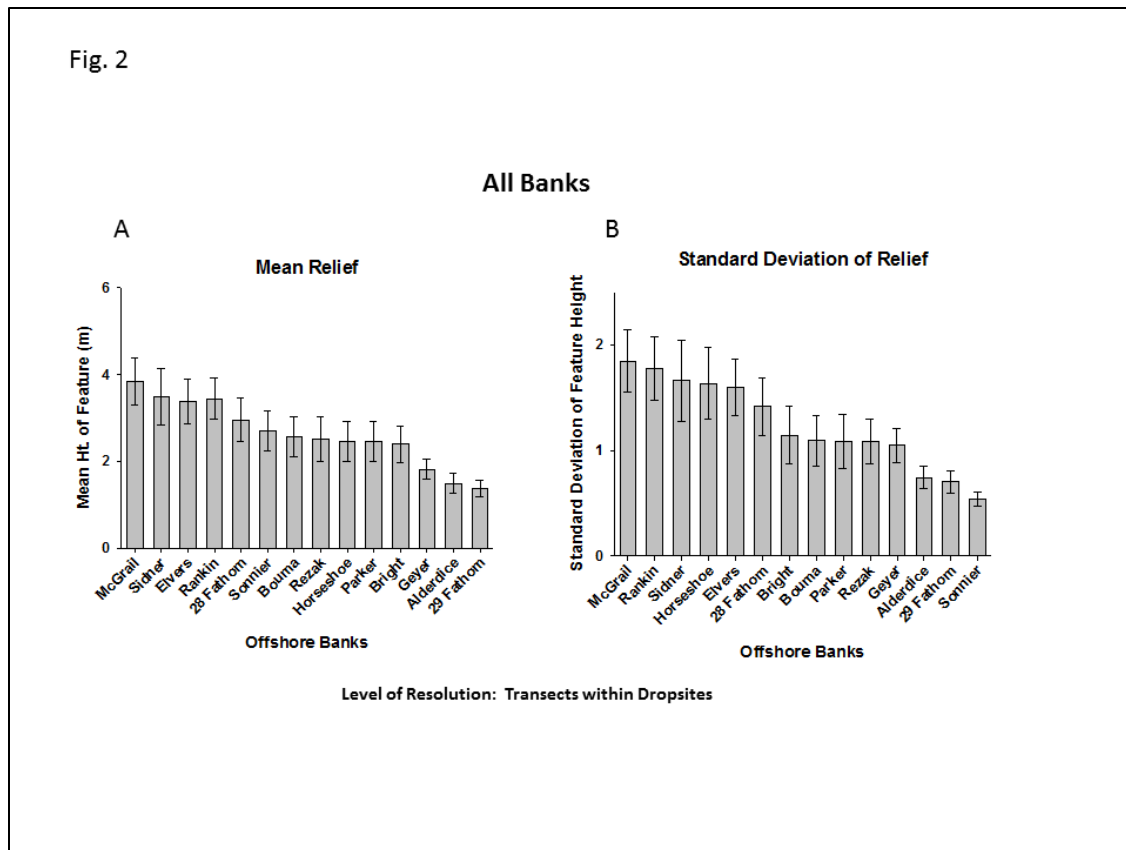


Figure 2. Benthic relief on all 14 study banks, shown from largest to smallest. Relief estimated by (A) mean and (B) SD values for each bank. Means calculated on relief values for 5 transects per drop-site, and 10 drop-sites per bank. 95% confidence limits also shown. Significant difference between banks using mean heights ($p < 0.001$, nested ANOVA; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests) and also between dropsites ($p < 0.001$). Significant difference between banks as well using SD of heights ($p < 0.001$, nested ANOVA) and between dropsites ($p < 0.001$).

3.1.2 Relief at the Spatial Scale of Drop-site and Transect: Exemplary Banks

Relief measures calculated for each of the 10 drop-sites within each bank have been graphed in detail by bank. We examined these data and identified the two banks that possessed drop-sites possessing the lowest and highest mean relief values. These were 29-Fathom and Sidner Banks, respectively. To simplify comparisons, we also chose a bank which possessed intermediate mean relief values at the drop-site level of resolution to exemplify banks of intermediate relief at this spatial scale. This was Bright Bank. These three banks received detailed statistical analyses.

Sidner Bank exhibited its lowest mean relief in Drop-site #5 - 2.5 m. Drop-site #6, on the other hand, had the highest mean of 6.5 m (Fig. 3a). Sidner exhibited a significant difference in mean height between drop-sites ($p < 0.01$, nested ANOVA), with only a small number of drop-sites being significantly different from each other ($p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests; Table 3). Mean relief values were more variable at the transect level of spatial resolution than at the drop-site level ($p < 0.001$, nested ANOVA). Fig. 3b reveals a wide

range of mean relief values at Sidner at the transect level of resolution, with a mean relief value in Transect #1, Drop-site #10 on this bank of 11.0 m. By comparison, the lowest relief value on the Sidner Bank (Drop-site #5, Transect #3) was 0.8 m (Fig. 3c). This represents a broad range. Interestingly, there were no significant differences between drop-sites when using the SD as the relief metric ($p > 0.05$, ANOVA). The smallest SD relief value for individual drop-sites was 1.0 m (Drop-Site #5) and the highest 3.2 m (Drop-site #6; Fig. 4a).

Table 3. Multiple pair-wise comparisons in bottom relief between transects on Sidner Bank.

Relief calculated as mean of relief within a transect. Five transects were sampled per drop-site and 10 drop-sites per bank. Transect means ordered in ascending manner. Significant differences between transects indicated via an asterisk (*; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests). An empty space signifies no significant difference. Only significantly different transects are shown.

Transect Number	Transect																																																											
	18	34	3	42	40	41	44	39	2	10	24	36	35	13	48	19	33	14	47	12	20	4	11	21	15	32	17	49	45	1	16	28	9	7	38	8	37	30	5	27	31	26	29	6	46															
23	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*									
43										*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*									
50										*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*								
22											*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*								
25											*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
18												*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
34													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
3													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
42													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
40													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*						
41													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*						
44													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*						
39													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
2													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
10													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
24													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
36													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
35													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
13													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
48													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
19													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*				
33													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*				
14													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*				
47													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*				
12													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*				
20													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
4													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
11													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
21													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
15													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
32													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
17													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
49													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
45													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
1													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
16													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
28													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
9													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
7													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
38													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
8													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
37													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
30													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
5													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
27													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
31													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
26													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
29													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
6													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

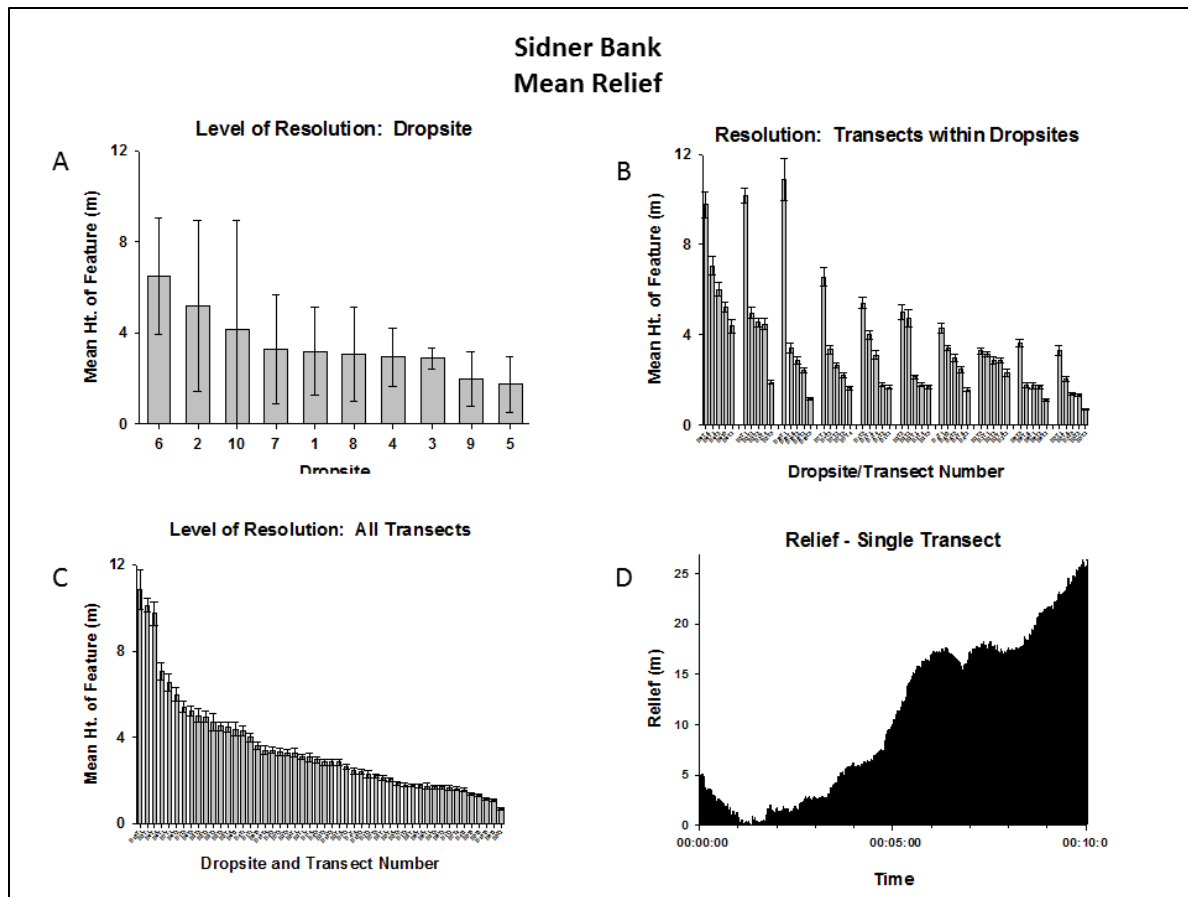


Figure 3. Relief on Sidner Bank, the bank determined to have the highest values of such.

Data shown for means, ordered from highest to lowest, (A) by drop-site; (B) by transect, grouped by drop-site; and (C) by transect in descending order, independent of drop-site. Means shown with 95% confidence limits. Significant difference between drop-sites ($p < 0.01$, nested ANOVA; $p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests) and transects within drop-sites ($p < 0.01$, nested ANOVA). (D) provides an example of the single transect on this bank with the highest relief.

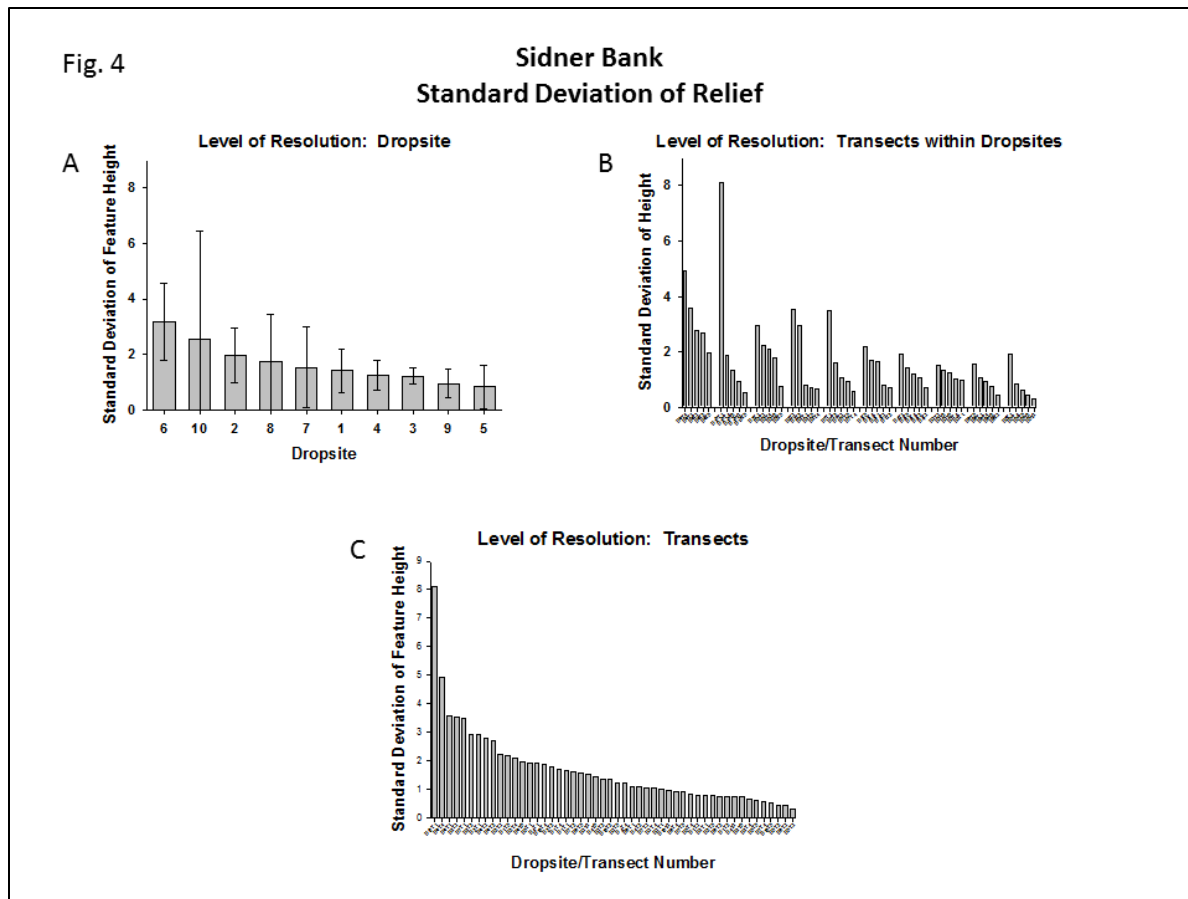


Figure 4. Benthic relief on Sidner Bank.

Data shown for SD of relief, ordered from highest to lowest (A) by dropsite; (B) by transect, grouped by drop-site; and (C) by transect in descending order, independent of drop-site. 95% confidence limits also shown. No significant differences between drop-sites ($p > 0.05$, ANOVA).

At the other end of the spectrum, 29-Fathom Bank exhibited the lowest mean relief of all banks. Mean relief varied only mildly between drop-sites, with Transect #10 having the lowest mean relief of 1.2 m and Transect #2 having the highest at 2.2 m (Fig. 5a). Indeed, there was no significant difference in mean relief between drop-sites ($p > 0.05$, ANOVA). Mean relief values were generally consistent between and within drop-sites (Fig. 5b&c). On the other hand, the overall pattern yielded by the SD index revealed highly significant differences between drop-sites ($p < 0.001$, ANOVA, Fig. 6a). The SD relief values varied from 0.7 m to 1.1 m, with a number of transects being significantly different from each other ($p < 0.05$, multiple comparisons among means, T', T-K, and GT2 test, Figs. 6b&c, Table 4). Once again, this suggests that SD is a more sensitive indicator of relief than the mean.

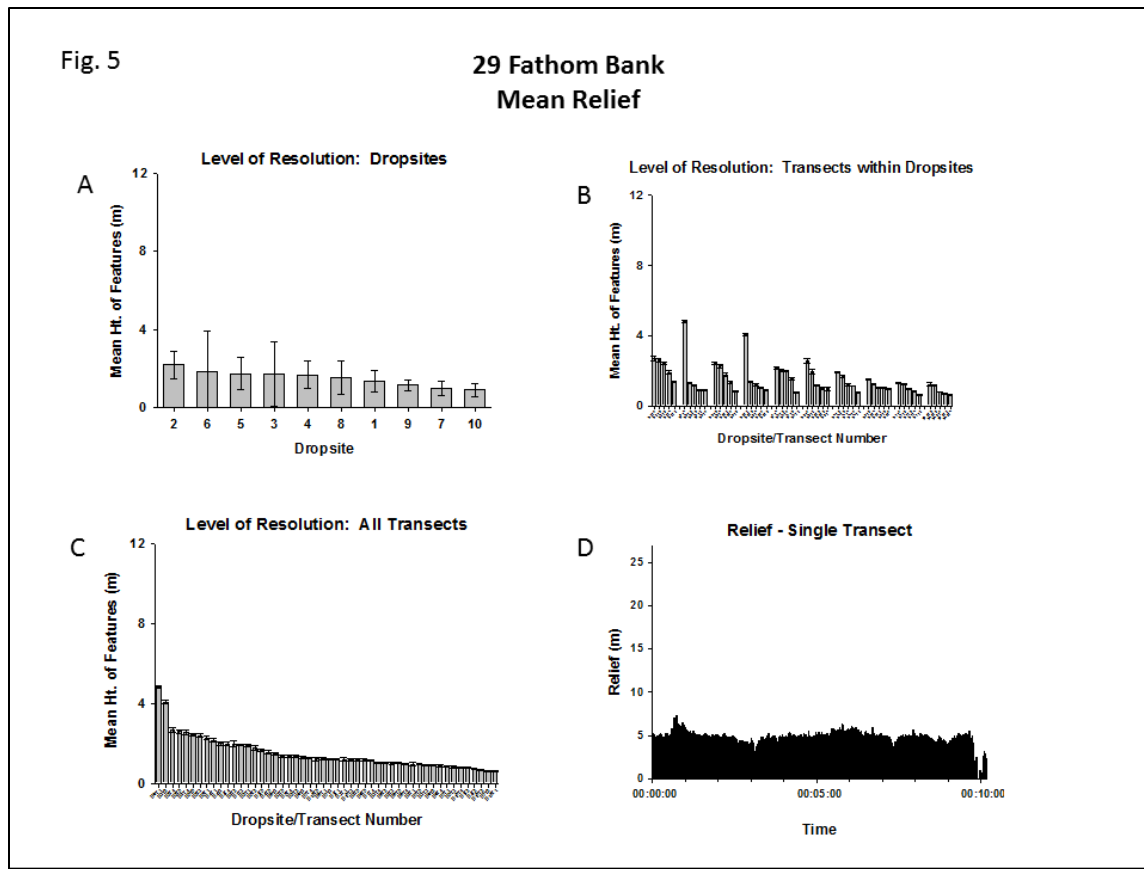


Figure 5. Benthic relief on 29 Fathom Bank, the bank determined to have the lowest relief of the 14 surveyed.

Data shown for mean, ordered from highest to lowest (A) by drop-site; (B) by transect, grouped by drop-site; and (C) by transect in descending order, independent of drop-site. Means shown with 95% confidence limits. No significant difference in relief between drop-sites ($p > 0.05$, ANOVA). (D) provides an example of the single transect on this bank with the highest relief.

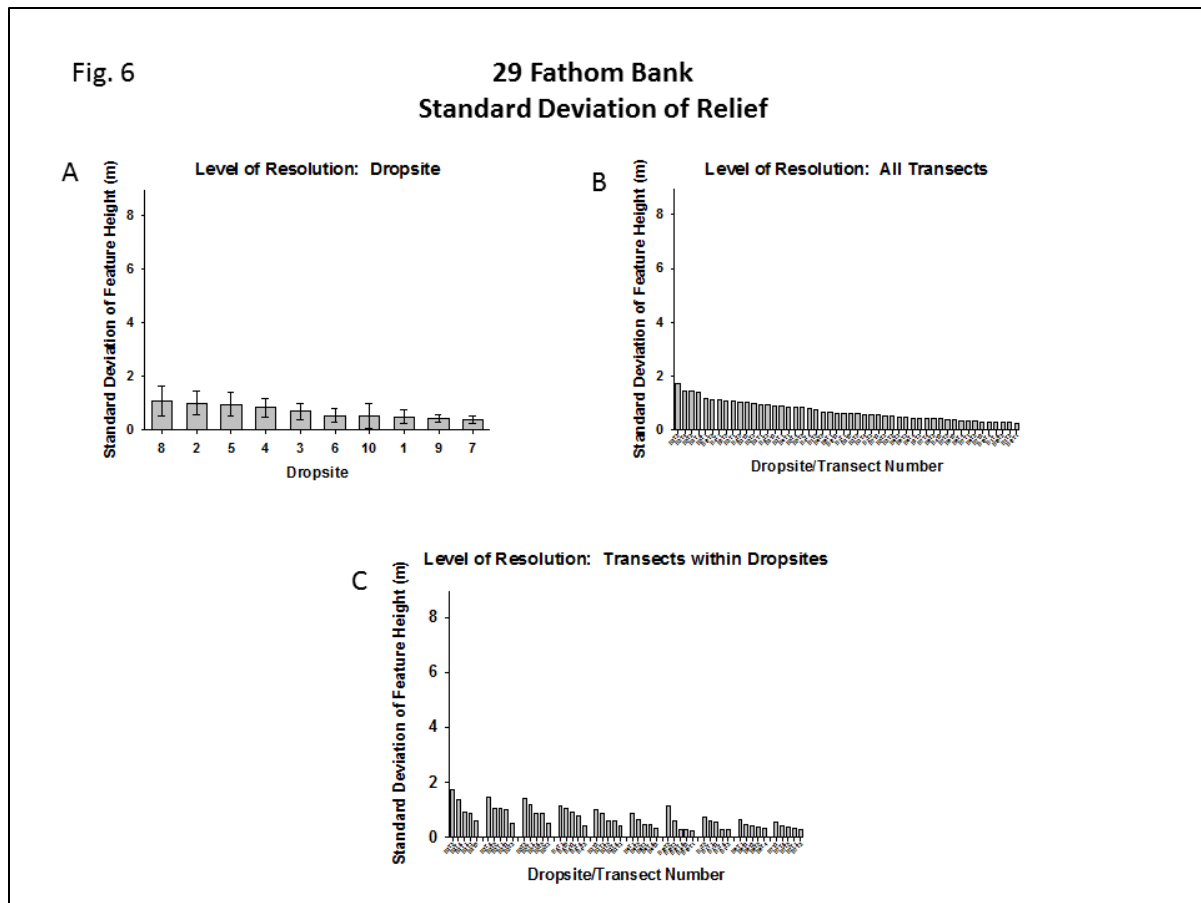


Figure 6. Benthic relief on 29 Fathom Bank.

Data shown for the SD of relief, ordered from highest to lowest (A) by drop-site; (B) by transect, grouped by drop-site; and (C) by transect in descending order, independent of drop-site. 95% confidence limits also shown. Significant difference between drop-sites ($p < 0.001$, ANOVA; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests).

As mentioned earlier, Bright Bank exhibited intermediate relief, serving as an example of other intermediate relief banks. Drop-sites varied significantly from each other ($p < 0.001$, nested ANOVA), with a wide variety of drop-sites being significantly different from each other ($p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests). The range of mean relief values varied from 1.5 m at Drop-site #1 to 5.1 m at Drop-site #10 (Fig. 7a). At the individual transect level, mean relief varied widely as well (Fig. 7c), with values ranging widely between 0.5 m and 8.5 m. Transects within drop-sites were significantly different from each other ($p < 0.001$, nested ANOVA). Relief as measured by SD at the spatial scale of drop-site ranged from 0.8 m to 2.6 m, being less variable than mean relief. There was a significant difference in SD values between drop-sites ($p < 0.001$, ANOVA; $p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests, Table 5). Similar variability and patterns were observed at the spatial scale of transects within drop-sites (Fig. 8b), with relief as measured by SD varying within the transects between 0.2 m and 5.0 m (Fig. 8c).

Table 5. Multiple pair-wise comparisons in bottom relief between transects on Bright Bank.

Index calculated as mean. Five transects were sampled per drop-site and 10 drop-sites per bank. Transect means ordered in ascending manner. Significant differences between transects indicated by an asterisk (*; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests). An empty space signifies no significant difference. Only significantly different transects are shown.

Trans.	Transect Numbers																																																														
No.	12	5	2	37	7	35	38	8	33	27	26	4	45	41	20	17	6	40	42	10	9	11	32	31	34	44	19	50	28	29	25	24	18	47	21	43	48	30	49	23	22	46																					
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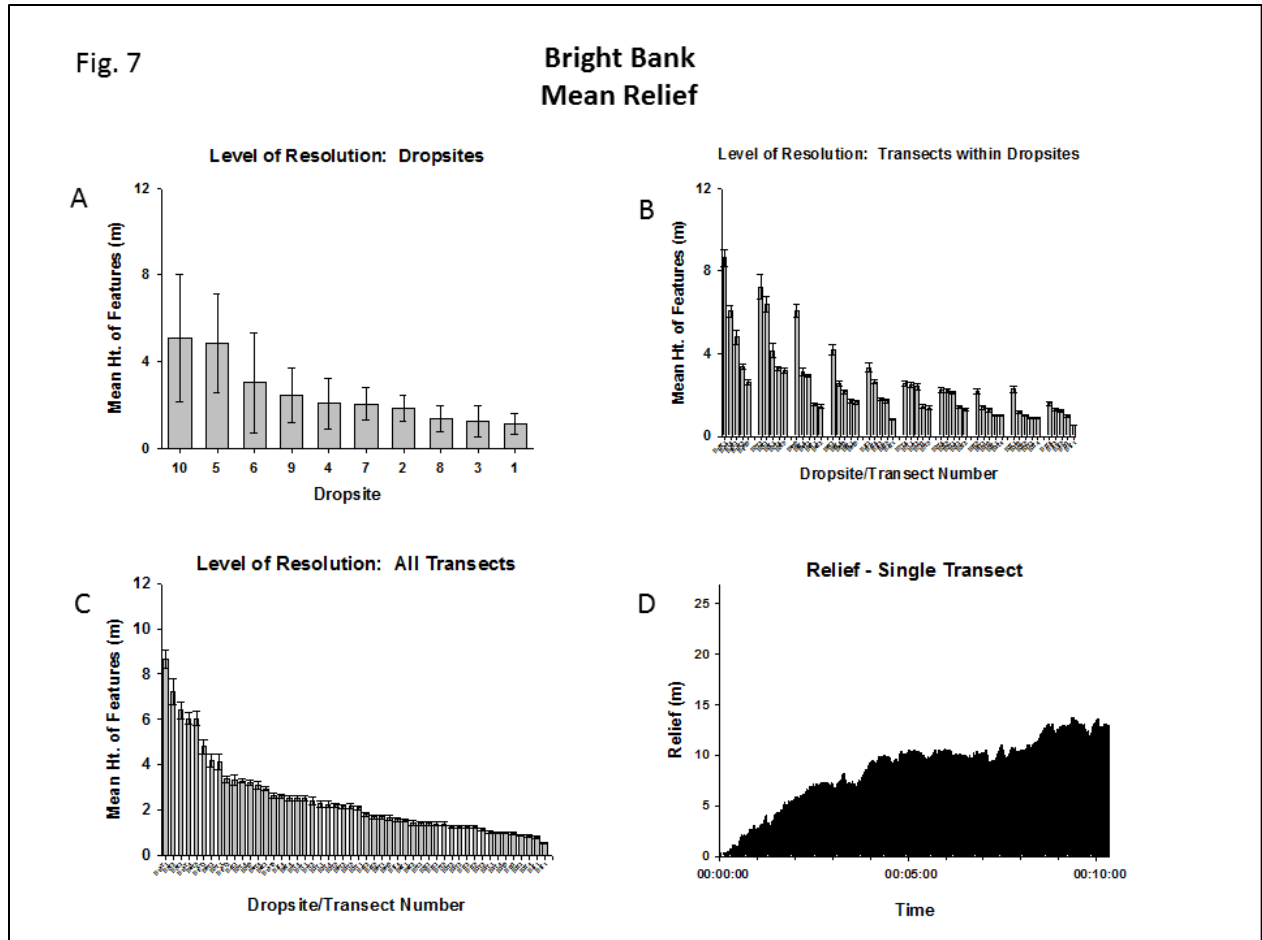


Figure 7. Benthic relief on Bright Bank, the bank determined to be intermediate in relief of the 14 banks surveyed.

Data shown for mean relief, ordered from highest to lowest (A) by drop-site; (B) by transect, grouped by drop-site, and (C) by transect in descending order, independent of drop-site. Means shown with 95% confidence limits. Drop-sites significantly different from each other ($p < 0.001$, nested ANOVA; $p < 0.05$, multiple comparisons among means, T', T-K, and GT2 tests), and transects within drop-sites significantly different from each other ($p < 0.001$, nested ANOVA). (D) provides an example of the single transect on this bank with the highest relief.

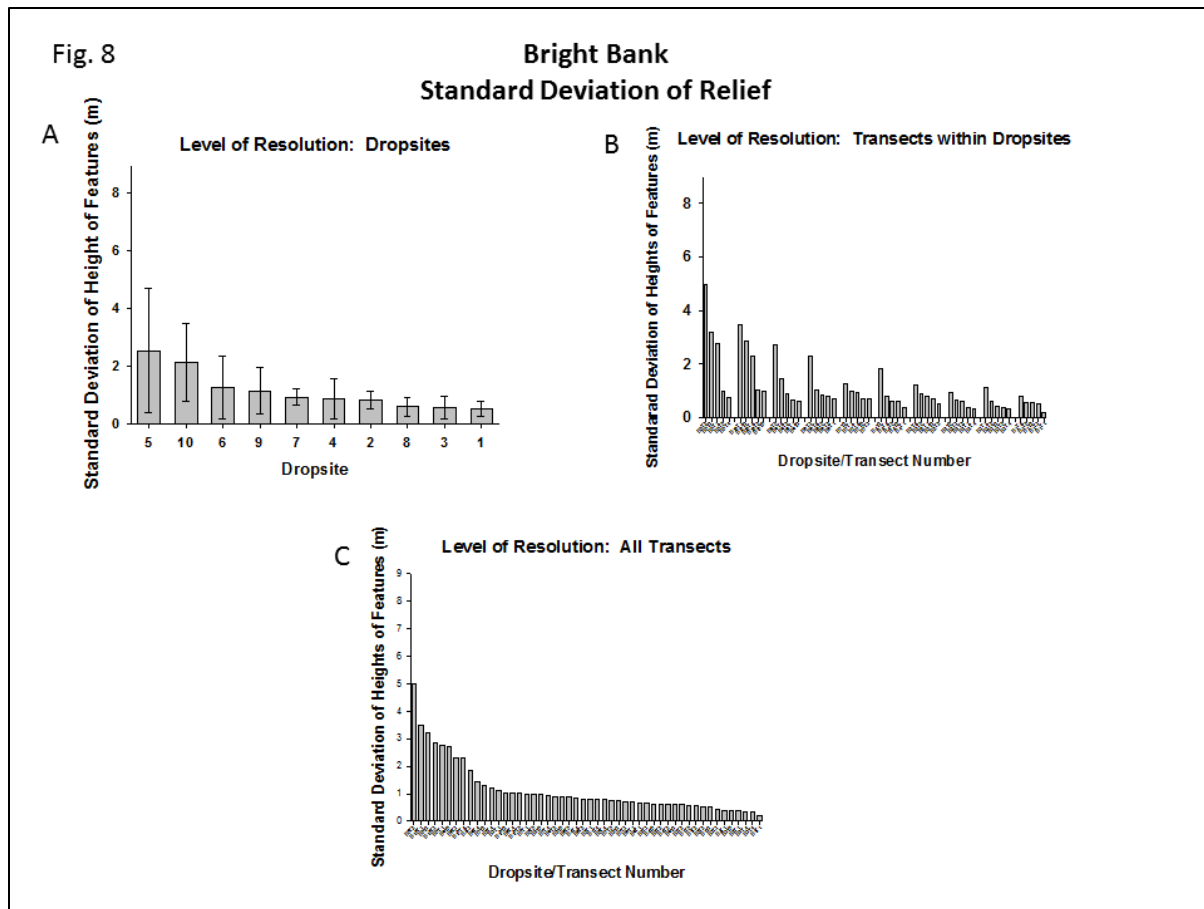


Figure 8. Benthic relief on Bright Bank.

Data shown for the SDR, ordered from highest to lowest (A) by drop-site; (B) by transect, grouped by drop-site; and (C) by transect in descending order, independent of drop-site (lower panel). 95% confidence limits also shown. Significant difference between drop-sites ($p < 0.001$, ANOVA; $p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests).

3.1.3 Remaining Banks

The other 11 banks exhibited patterns of relief similar to the above three banks, depending upon whether their values were low, intermediate, or high. This was the case whether measured by mean or SD. Figures 9 to 14 present relief values calculated by mean and SD, respectively, for the remaining banks, which are presented at the drop-site level. The banks are presented in ascending order of relief, as determined by the largest drop-site value.

Sonnier and Alderdice Banks were low and highly consistent and predictable in relief. Sonnier Bank exhibited no significant difference in relief between drop-sites, whether measured by mean relief or SD ($p > 0.05$, ANOVA, Figs. 9a & b, respectively). Alderdice Bank also exhibited no significant difference between drop-sites when measured by mean relief ($p > 0.05$, ANOVA, Fig. 9c); however, when relief was measured by SD, there was a significant difference between drop-

sites ($p < 0.05$, ANOVA). In this case, only one drop-site was significantly different from one other ($p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests, Fig. 8d).

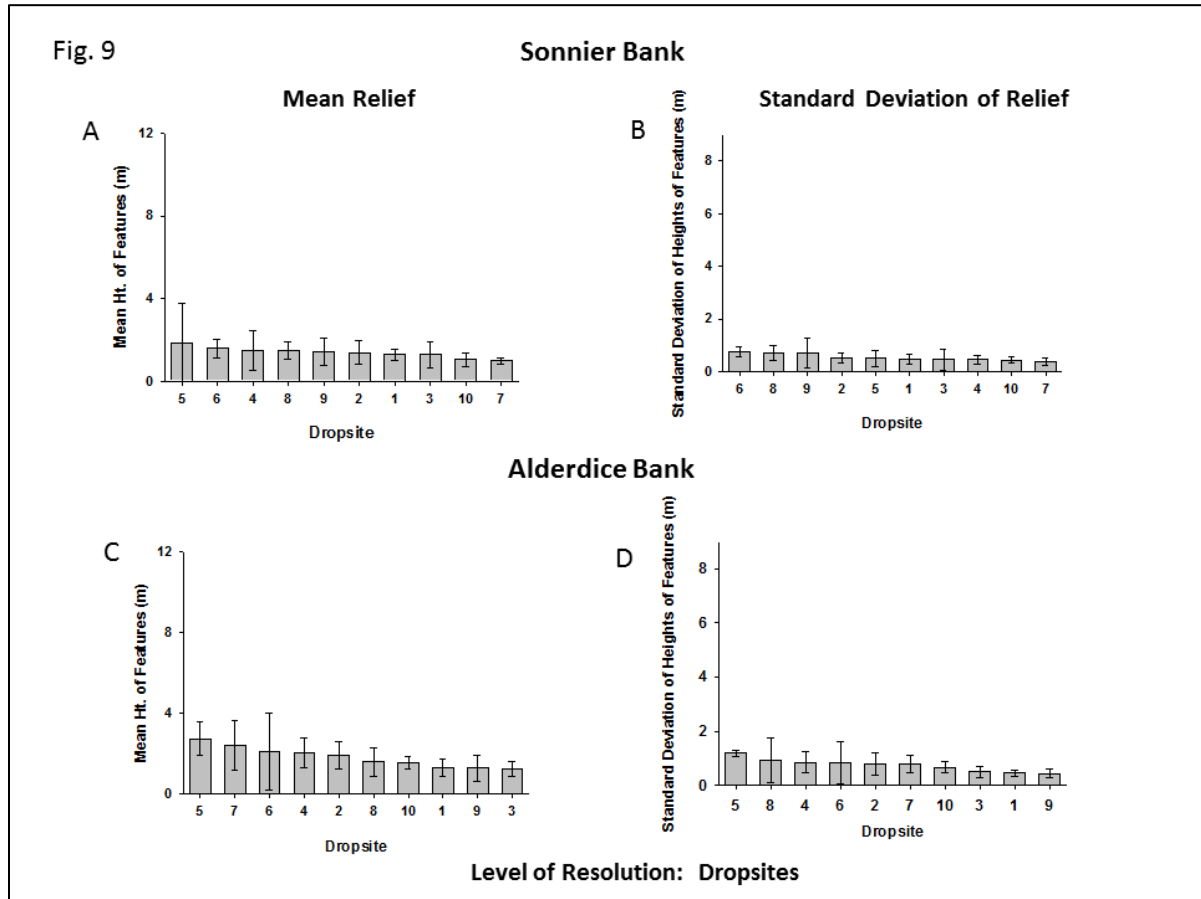


Figure 9. Benthic relief for Sonnier Bank (A&B) and Alderdice Bank (C&D), respectively.

These banks were determined to have intermediate relief in relation to the 14 banks surveyed. Data shown for (A&C) mean relief, ordered from highest to lowest by drop-site; and (B&D) by SD, also ordered from highest to lowest by drop-site. 95% confidence limits also shown.

Rezak and Bouma Banks, intermediate relief banks, both exhibited highly significant differences between drop-sites. For Rezak, this was the case using mean relief as a measure ($p < 0.001$, ANOVA, Fig. 10a). There, drop-sites #1, 4, and 5 were found to be significantly different than 2, 3, and 8 ($p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests). There was also a highly significant difference in relief values between drop-sites when measured by the SD ($p < 0.01$, ANOVA, Fig. 10b). Here, only transects #3 and 8 were significantly different from #1 ($p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests). There were significant differences in mean relief between drop-sites on Bouma Bank ($p < 0.05$, ANOVA, Fig. 10c). Those differences were more significant, however, when SD was used as a measure of relief ($p < 0.01$, Fig. 10d), with a number of transects being significantly different than others ($p < 0.05$,

multiple comparisons between means, T', T-K, and GT2 tests) – another indicator of the higher sensitivity of this index.

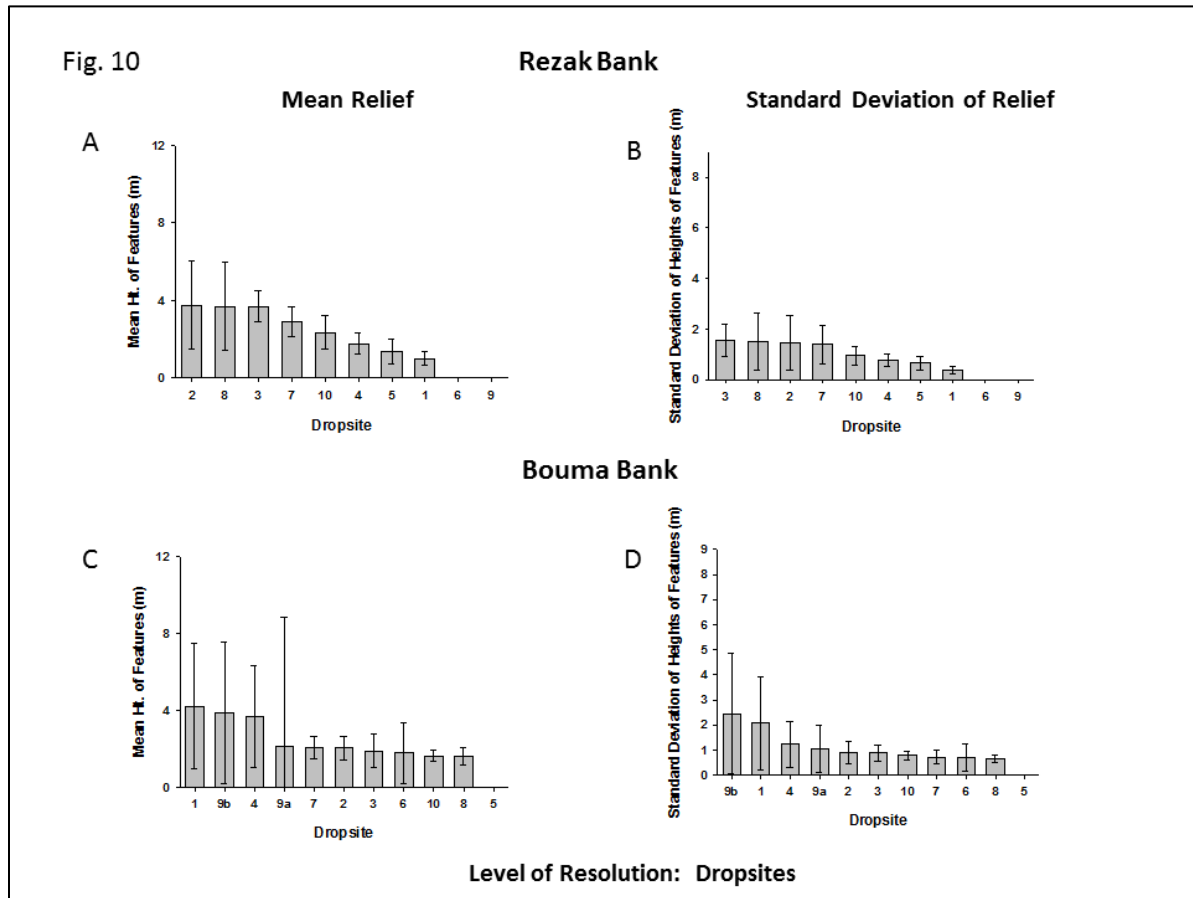


Figure 10. Benthic relief on Rezak Bank (A&B) and Bouma Bank (C&D), respectively. These banks were determined to have intermediate relief values in relation to the 14 banks surveyed. Data shown for mean relief (A&C), ordered from highest to lowest by drop-site; and by SDR (B&D), also ordered from highest to lowest by drop-site. 95% confidence limits also shown.

28-Fathom Bank and Horseshoe Bank were both intermediate in their relief values but varied between each other in degree of variability of relief. For example, 28-Fathom Bank showed no significant differences in mean relief between drop-sites ($p > 0.05$, ANOVA, Fig. 11a). SD of relief, however, varied highly significantly between drop-sites ($p < 0.01$, ANOVA), with Transect #10 being significantly different from 5 of the other transects ($p < 0.05$, multiple comparisons between means, T', T-K, and GT2 tests, Fig. 11b). Mean relief was highly significantly different between drop-sites on Horseshoe Bank ($p < 0.001$, ANOVA, Fig. 11c), with a number of transects being significantly different from each other ($p < 0.05$, multiple comparisons tests, Fig. 11d). The same patterns of significant differences were observed when SD was used as an indicator of relief.

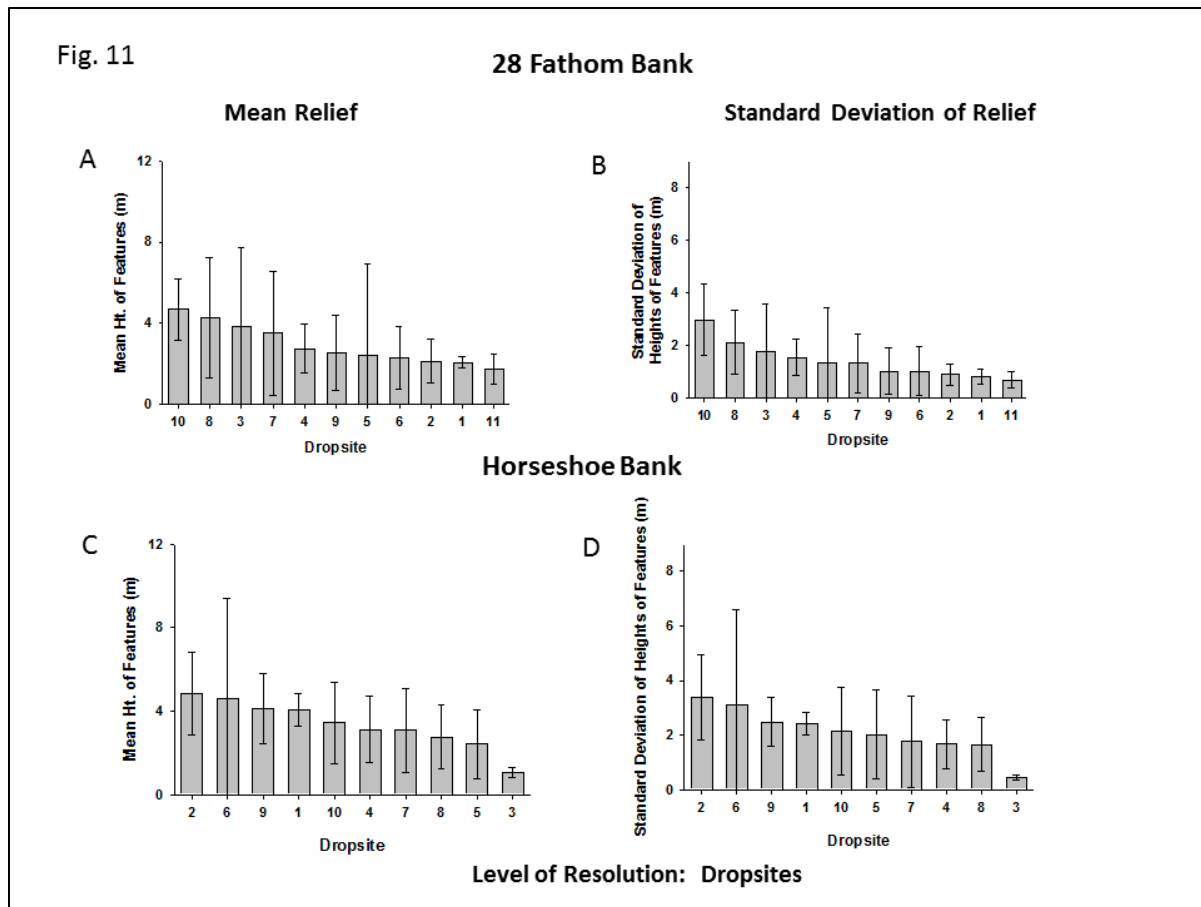


Figure 11. Benthic relief values for 28-Fathom Bank (A&B) and Horseshoe Bank (C&D), respectively.

These banks were determined to have intermediate relief values in relation to the 14 banks surveyed. Data shown for mean, ordered from highest to lowest by drop-site (A&C); and for SDR (B&D), also ordered from highest to lowest by drop-site. 95% confidence limits also shown.

Geyer and Elvers Bank were also different from each other in the consistency of variability in their relief patterns. In this case, Geyer exhibited highly significantly different mean relief values between drop-sites ($p < 0.001$, ANOVA, Fig. 12a), with a number of drop-sites varying significantly from each other ($p < 0.05$, multiple comparisons). This pattern was repeated when using SD as an indicator of relief ($p < 0.01$, ANOVA; $p < 0.05$, multiple comparisons, Fig. 12b). This was not the case with Elvers Bank. Mean relief did not vary significantly between drop-sites there ($p > 0.05$, ANOVA, Fig. 12c). SD of relief, however, did vary significantly between drop-sites ($p < 0.05$, ANOVA). This was driven, however, only by differences between two transects ($p < 0.05$, multiple comparisons, Fig. 12d).

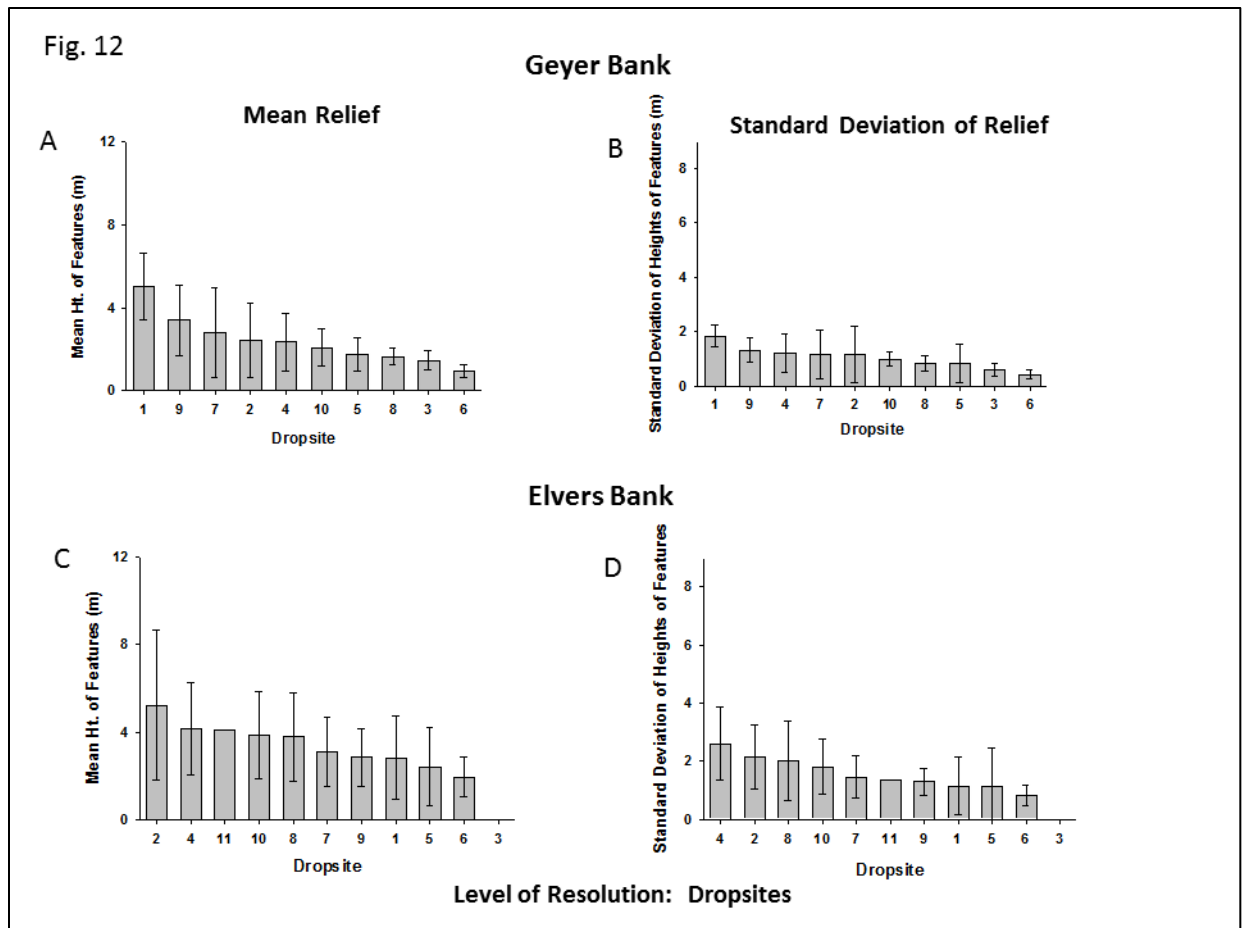


Figure 12. Benthic relief for Geyer Bank (A&B) and Elvers Bank (C&D), respectively. These banks had intermediate relief values in comparison to the 14 banks surveyed. Data shown for mean relief, ordered from highest to lowest by drop-site (A&C); and by SDR, also ordered from highest to lowest by drop-site (B&D). 95% confidence limits also shown.

McGrail, Parker, and Rankin Banks all had had high values of mean relief (Fig. 13a) and SD (Fig. 13b) and, like the last four reefs, varied significantly in their patterns of relief between drop-sites. McGrail exhibited no significant differences between drop-sites ($p > 0.05$, ANOVA). Parker Bank, on the other hand, exhibited highly significant differences in both mean relief (Fig. 13c) and SD (Fig. 13d, $p < 0.001$, ANOVAs), and showed significant differences between a number of transects, using both indices ($p < 0.05$, multiple comparisons). Rankin Bank, like Parker, had highly significant differences in both mean relief (Fig. 14a) and SD (Fig. 14b; $p < 0.001$, ANOVAs), with a variety of transects being significantly different from each other ($p < 0.05$, multiple comparisons).

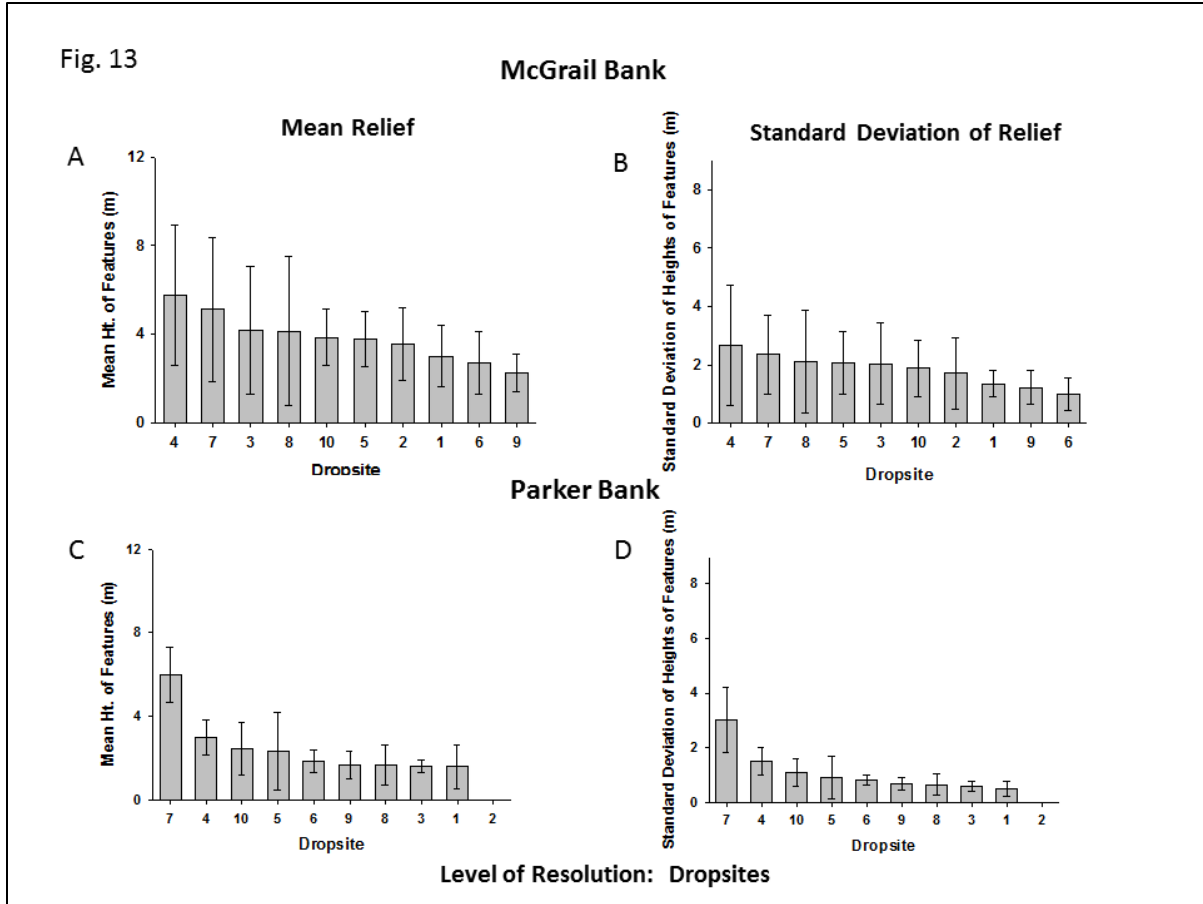


Figure 13. Benthic relief on McGrail Bank (A&B) and Parker Bank (C&D), respectively. These banks had intermediate levels of relief in comparison to the 14 banks surveyed. Data shown as mean, ordered from highest to lowest by drop-site (A&C); and by SD, also ordered from highest to lowest by drop-site (B&D). 95% confidence limits also shown.

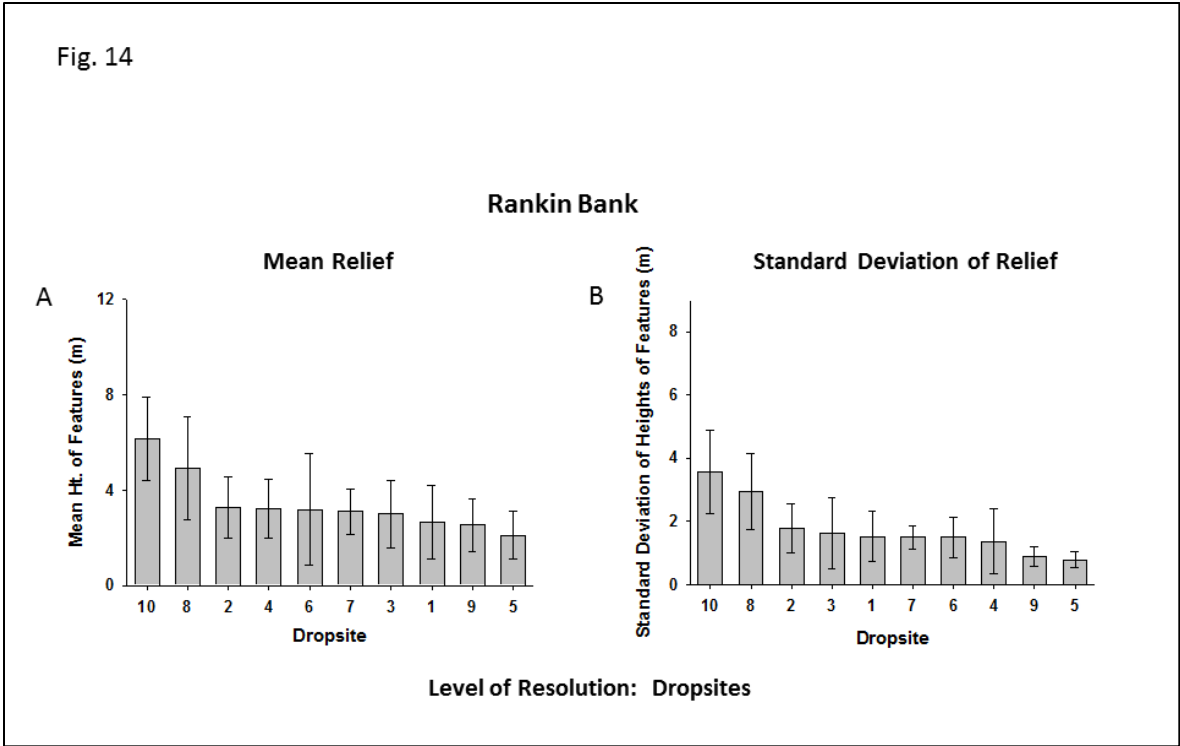


Figure 14. Benthic relief on Rankin Bank. This bank was determined to have intermediate relief values with respect to the 14 banks surveyed. Data shown for mean relief, ordered from highest to lowest by drop-site (A); and by SDR, also ordered from highest to lowest by drop-site (B). 95% confidence limits also shown.

A comparison of the significant differences between drop-sites across all banks revealed that there was no pattern in predictability of relief between the banks, except perhaps in the three lowest relief banks: 29-Fathom, Sonnier, and Alderdice Banks (Table 6). That is, the variability in relief between drop-sites was either not significant or marginally significant there.

Table 6. Summary of significant differences in relief between drop-sites on each of the banks.

Analysis used was an ANOVA. Data shown for both the mean relief and SD indicators. n.s = no significant difference; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Data indicate that variability in relief within a bank at the drop-site level of resolution can be unpredictable, irrespective of index used, except in low relief situations.

Bank	Relief Index	
	Mean	SD
Sidner	*	n.s.
Rankin	***	***
Parker	***	***
McGrail	n.s.	n.s.
Elvers	n.s.	*
Geyer	***	**
Horseshoe	***	***
Bright	***	***
28-Fathom	n.s.	**
Bouma	*	**
Rezak	***	**
Alderdice	n.s.	*
Sonnier	n.s.	n.s.
29-Fathom	n.s.	*

3.1.4 Large-Scale Geographic Patterns

The 14 study banks covered 215 km along the shelf edge and a total area of ~5,400 km², allowing us to analyze relief for broader geographic patterns. When relief was measured by the mean index and plotted against latitude, a clear negative correlation emerged. Relief on these banks was significantly higher at lower latitudes and decreased as one moved northward across the study area towards the shore (Fig. 15a). That is, there was a significant decrease in relief from south to north using the mean as an index ($r = 0.442$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Model II regression, $Y = 114.69 - 0.40X$). The same pattern emerged using SD as a descriptor (Fig. 15b; $r = 0.442$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Model II Regression, $Y = 66.17 - 2.32 X$).

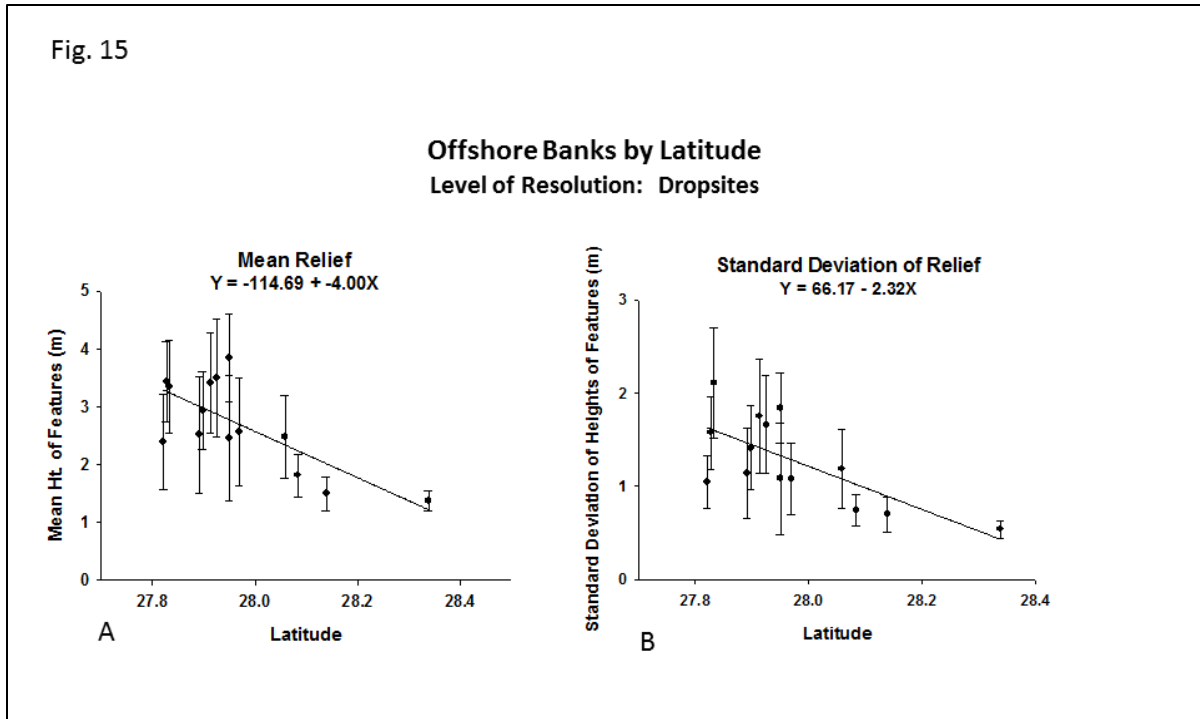


Figure 15. Latitudinal pattern in benthic relief for all 14 banks surveyed.

(A) Mean relief. (B) SDR. 95% confidence limits shown also shown. Significant decrease in relief from south to north (Index = Mean: $r = 0.442$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Model II regression, $Y = 114.69 - 0.40X$. Index = SD: $r = 0.442$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Model II Regression, $Y = 66.17 - 2.32X$).

When relief was plotted against longitude, a more complex pattern emerged. Using the mean as a measure, relief peaked in the west, south of Port Arthur and Lake Sabine, Texas; decreased off Cameron, Louisiana to the east; and then increased again further east off Grand Chenier, LA. Finally, it decreased again off Vermillion Bay, Louisiana (Fig. 16a). This non-linear change in relief from west to east was highly significant ($r = 0.215$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Polynomial Regression, $Y = 1.24 \times 10^6 - 4.01 \times 10^4 X - 431.4X^2 - 1.5X^3$). This pattern was mimicked when SD was used as a descriptor, except the pattern was more exaggerated (Fig. 16b; $r = 0.330$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Polynomial Regression, $Y = -1.18 \times 10^6 - 3.8 \times 10^4 X - 412.6 X^2 - 1.48$). There would appear to be two zones where relief is reduced along this study tract – one in the west and one in the east.

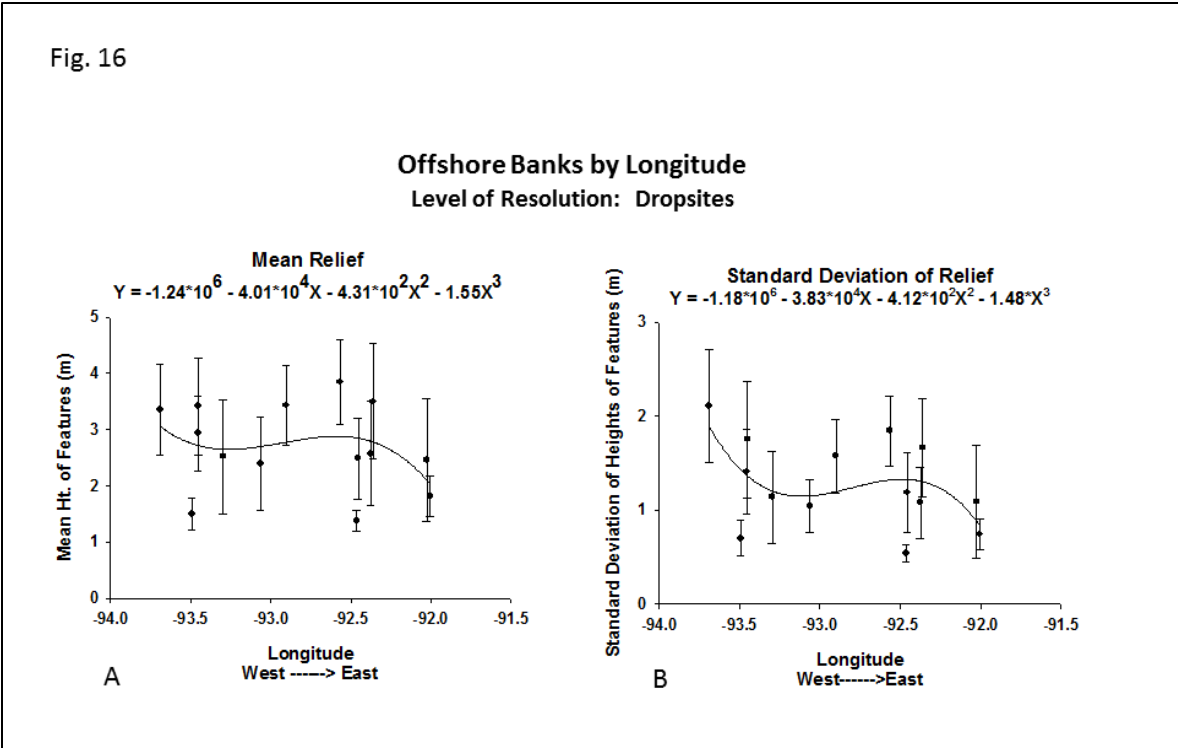


Figure 16. Longitudinal pattern of relief on all 14 banks surveyed. (A) Mean relief. (B) SDR. 95% confidence limits also shown. Significant non-linear change in relief from west to east (Index - Mean Height: $r = 0.215$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Polynomial Regression, $Y = 1.24 \times 10^6 - 4.01 \times 10^4 X - 431.4 X^2 - 1.5 X^3$. Index - SD of height: $r = 0.330$, $p < 0.01$, Pearson's Product-Moment Correlation; $p < 0.001$, Polynomial Regression, $Y = -1.18 \times 10^6 - 3.8 \times 10^4 X - 412.6 X^2 - 1.48$).

When these data are placed into a 3-D context and displayed, the geographic pattern becomes more evident. Using mean relief as an indicator, an increase at lower latitudes to the west is revealed, along with a somewhat smaller peak in the east at higher latitudes (Fig. 17a). There is reduced relief between these two peaks, along the shelf edge, and in the southeast of the study area, near the shelf edge. A parallel pattern emerged using the SDR (Fig. 17b).

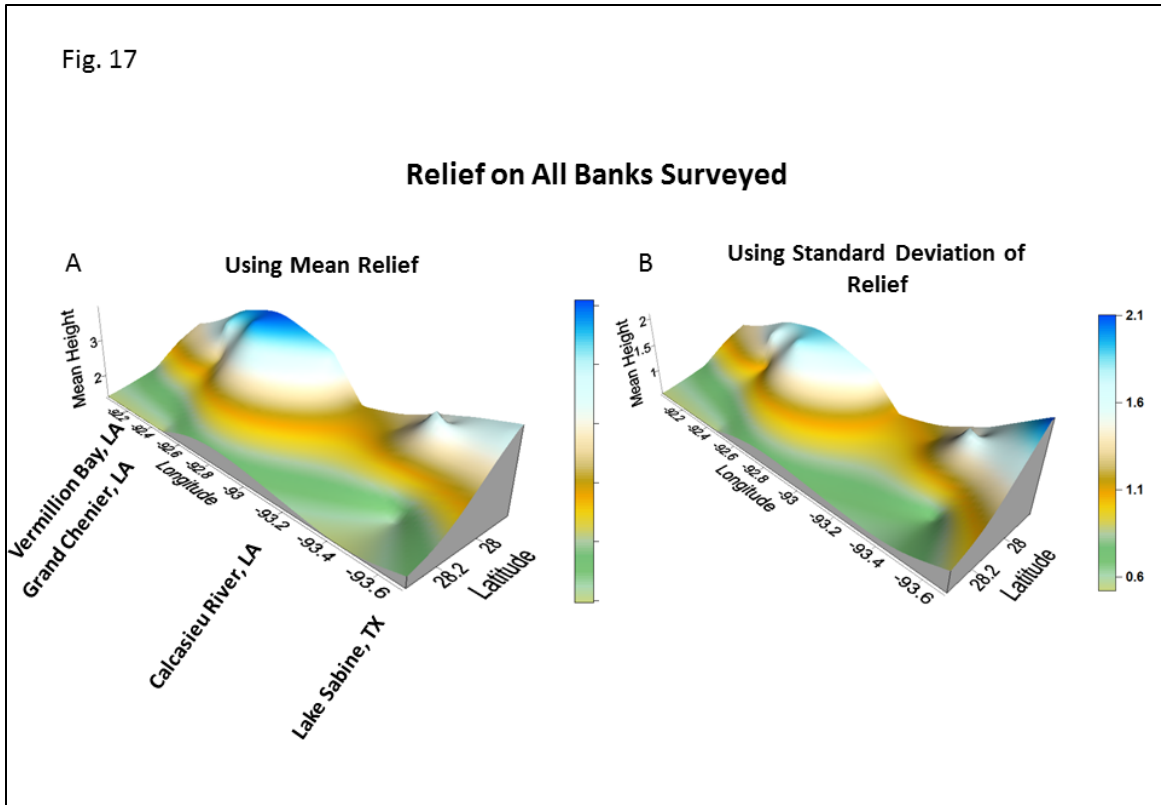


Figure 17. 3-D benthic relief of 14 banks surveyed in the north-central Gulf at the edge of the continental shelf.

Perspective is from shore, with east on the left and west on the right, to facilitate view of changes. Descriptors used to estimate relief were (A) mean relief and (B) SDR. High points in relief are at the edge of the continental shelf, south of Port Arthur, Texas and Grand Chenier, Louisiana. Low points are south of Calcasieu Lake and Calcasieu River and Vermillion Bay and Atchafalaya River, Louisiana.

3.2 Patterns of Mesophotic Benthic Community Structure

3.2.1 Grouping of Banks: Dendrogram

PATN[©] produced a dendrogram illustrating how the banks were associated with each other, driven by the sessile epibenthic species community on each bank (Fig. 18). An array of dissimilarity values are shown on the top of the dendrogram. PATN[©] recommends that the square-root of the number of objects be used for the grouping cut-off point. In this case, we had 13 banks, for a square root of 3.6; thus, three groups were targeted. This approach resulted in 29 Fathom and Sonnier Banks defined as Bank Group #1. Geyer Bank was identified next to be the sole member of Bank Group #2. The remaining banks all fell into Bank Group #3 - Horseshoe, 28 Fathom, Bright, Alderdice, Bouma, Rankin, Elvers, McGrail, and Sidner Banks.

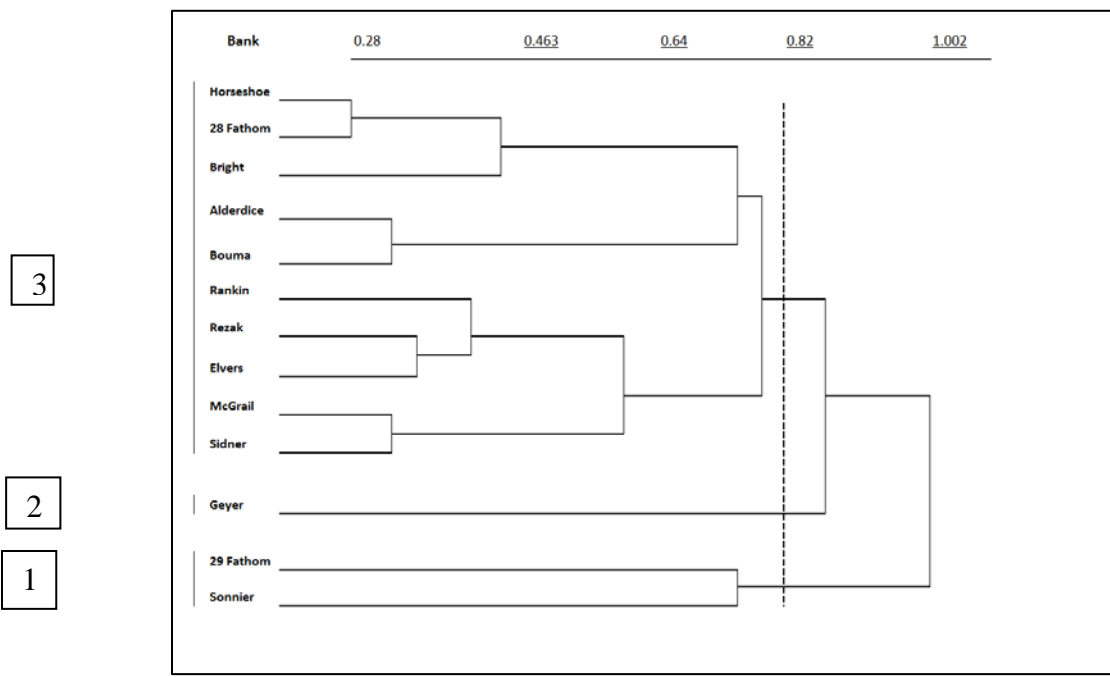


Figure 18. Dendrogram produced by PATN[®], illustrating groups of banks.

Bank Groupings determined by analysis of the structure of the sessile, epibenthic community on each bank. Three groups identified: Bank Group #1) 29 Fathom and Sonnier Banks; Bank Group #2) Geyer Bank; and Bank Group #3) Horseshoe, 28 Fathom, Bright, Alderdice, Bouma, Rankin, Rezak, Elvers, McGrail, and Sidner Banks.

3.2.2 Dissimilarity Matrix

PATN[®] also produced a dissimilarity matrix of the banks, based on the sessile epibenthic species and their abundances (Table 7). In this matrix, once again, 0.0 designates complete similarity, and 1.0 complete dissimilarity. Table 7 is consistent with the dendrogram results. For example, 29 Fathom Bank is described entirely by high dissimilarity numbers in its pair-wise comparisons with all other banks, ranging from 0.6926 to 0.9414. Sonnier Bank has similar values, ranging from 0.6926 to 0.9302. Geyer Bank, the stand-alone bank in its own group, also had high values of dissimilarity in its pair-wise comparisons, ranging from 0.6336 to 0.9024. The remaining 10 banks had, on average, low dissimilarity indices, ranging from 0.2835 to 0.8856.

Table 7. Dissimilarity matrix for all banks, based on all species of sessile epibenthic community structure.

All possible pair-wise comparisons shown. Data helped determine Bank Groups generated in the dendrogram shown in Fig. 2. Blue represents Bank Group #1, red represents Bank Group #2, and the remainder Bank Group #3.

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

3.2.3 Geographic Distribution

When graphed according to location, the banks within their groups reveal an interesting geographic pattern (Fig. 19). Bank Group #3, shown in red in the figure, occur approximately in a line, extending from the western section of the study region E-NE to the eastern side. This trajectory tracks the edge of the continental shelf in the northern Gulf.

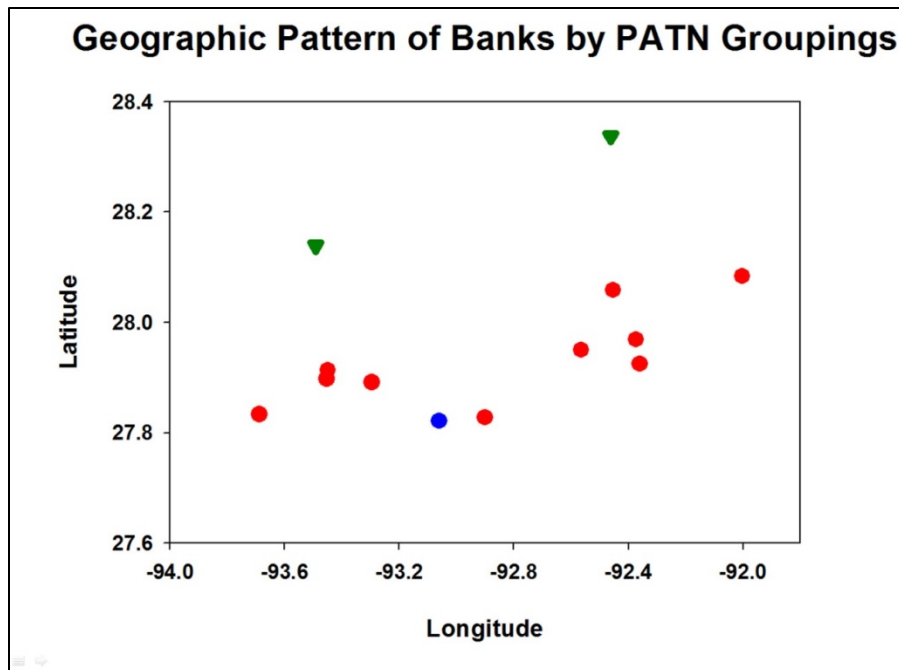


Fig. 19. A graph of the geographic study banks' locations.

The colors represent the Bank Groups identified by PATN[®] as being similar. The two northernmost banks (29 Fathom and Sonnier Banks; green triangles; Bank Group #1) occur shoreward, on the continental shelf, not at the shelf edge. The lone bank (blue circle; Bank Group #2) is Geyer Bank. The edge of the continental shelf runs roughly E-NE from the first bank on the left, following the majority of the banks (remainder of banks; red circles; Bank Group #3).

Bank Group #1, on the other hand, shown in green, occurred furthest north, extending N-NE across the study region. The banks in Group #1 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).

The lone site in Bank Group #2, Geyer Bank, occurs at the shelf edge like Elvers and the nine other banks in Bank Group #1.

3.2.4 Species Groupings and Differential Species Distributions, by Bank

Tables 8 and 9 show all of the species encountered on these banks and how the program (PATN[®]) placed them into different Species Groups. The amount of influence that each of these species had on defining a Bank and a Bank Group could then be discerned. A species could influence several banks simultaneously, but usually at different degrees of intensity. The range of abundance impact is shown for each species and varied between 0.0 and 1.0, where 1.0 represents the highest abundance of any species on a given bank.

most abundant species on that bank, yielding a comparative abundance. Most abundant species along with other primary species driving assignment of a bank to a Bank Group (0.81–1.0) are shown in bold. Data analyzed using the Agglomerative Hierarchical treatment (see Fig. 18). Comparative abundances have been color-coded using increasingly dark shades of green, falling into four categories: $0.21 \leq 0.40$; $0.41 \leq 0.60$; $0.61 \leq 0.80$; and $0.81 \leq 1.0$, respectively. Data for fifth category of abundance, $0 \leq 0.20$, shown in Table 9.

Table 8 provides information on which sets of species are helping to characterize the benthic communities observed on the study banks, and differentiating between the banks in this way. This provides the biological aspect of habitat characterization for these species. Below, where we examine the relationship between the physical and biological aspects of these banks in concert, habitat characterization will become clearer as we observe how these two factors covary in space.

About Table 9: In comparison to Table 8 (primary contributing species), these species play a more minor role in their Species Groupings and thus in forcing allocation of the banks into Bank Groupings. Individual Column Standardization technique used to standardize each species entry within a bank, using the species with a maximum value as a comparative standard against which its abundance is compared proportionally (See Table 8 for explanation and further details).

Table 9. An overview of abundances of sessile epibenthic species, by bank.
 All species listed here fall in the $0 - \leq 0.20$ abundance category. Table generated by PATN[®],

Species or ID Code	Species or ID Code	Species or ID Code
Species Group 1	C	Echinoderm, ST16
A	<i>Chondrosia</i> sp. 1	Echinoderm, ST17
<i>Agaricia</i> sp.	Clam	Echinoderm, ST18
Algae, AL01	<i>Codium</i> sp.	Echinoderm, ST19
Algae, AL02	<i>Comactinia meridionalis</i>	Echinoderm, ST20
Algae, AL05	Coral, Colonial cup	<i>Ectoplaysia ferox</i>
Algae, AL07	Coral, Stony, S04	Eel
Algae, AL08	Coral, Stony, S07	<i>Erylus alleni</i>
Algae, AL09	Coral, Stony, S09	<i>Erylus trisphaera</i>
Algae, UnID	Coral, UnID	
<i>Anadyomene</i>	<i>Coronaster briareus</i>	G
Anemone	Crab	Gastropod
Anemone, AN2	Crinoid, CR01	Gorgonian, G03
Anemone, AN3	Crinoid, CR02	Gorgonian, G05
Anemone, AN5	Crinoid, CR06	Gorgonian, G06
<i>Anthomastus robusta</i>	Crinoid, CR08	Gorgonian, G07
Antipatharian, A01	Crinoid, CR09	Gorgonian, G08
Antipatharian, A02	Crinoid, CR11	Gorgonian, G09
Antipatharian, A03	Crinoid, CR14	Gorgonian, G10
Antipatharian, A06	Crustacean	Gorgonian, G11
Antipatharian, A07	<i>Cyphoma gibbosum</i>	Gorgonian, G14
Antipatharian, A08		Gorgonian, G15
Antipatharian, A11	D	
Antipatharian, A12	<i>Dictyonellidae</i>	H
Antipatharian, UnID	<i>Dictyota</i> sp.	<i>Hacelia superba</i>
<i>Antipathes atlantica</i>	<i>Diodogorgia nodulifera</i>	<i>Halichondria</i> sp.
<i>Aplysilla sulfurea</i>	<i>Diodogorgia stellata</i>	<i>Halichondria</i> sp. 1
Arrow crab	<i>Dysidea</i> sp.	<i>Halimena hancockii</i>
Ascidean, didemnid	<i>Dysideidae</i>	<i>Henricia sexradiata</i>
<i>Auletta sycinularia</i>		Hydroid, DFH8-10A
	E	Hydroid, DFH9-13C
B	Echinoderm, ST03	Hydroid, DFH11-12A
Basket star	Echinoderm, ST04	Hydroid, DFH11-21A
<i>Batzella rubra</i>	Echinoderm, ST06	Hydroid, H02
Bivalves	Echinoderm, ST09	Hydroid, H04
Brittle star	Echinoderm, ST10	Hydroid, H07
Bryozoan sp.	Echinoderm, ST12	Hydroid, H08
Bryozoan, white tangled	Echinoderm, ST13	Hydroid, H09
	Echinoderm, ST15	Hydroid, H14

Species or ID Code	Species or ID Code	Species or ID Code
I	Shrimp	Tunicate, T7
Invertebrate, UnID	Slit Shell	Tunicate, T9
	<i>Smenospongia</i> sp.	Tunicate, T10
L	Sp. 2, UnID	Tunicates
<i>Leptogogia</i> sp.	Sponge, Encrusting purple	
Lobster	Sponge, Encrusting white	U
	Sponge, glass	Urchin
M	Sponge, SP01	Urchin, U02
<i>Madracis brueggemanni</i>	Sponge, SP03	
<i>Mithrix hispidus</i>	Sponge, SP06	V
<i>Myrmekioderma gyroderma</i>	Sponge, SP08	<i>Ventricaria</i> sp.
	Sponge, SP11	<i>Ventricaria ventricosa</i>
N	Sponge, SP14	Vermetid mollusc
<i>Neopetrosia</i> sp.	Sponge, SP15	
<i>Niphates erecta</i>	Sponge, SP16	W
	Sponge, SP18	Worm, Featherduster
O	Sponge, SP19	Worm, Fireworm
<i>Oculina</i>	Sponge, SP20	Worm, Tube or Anemone, I01
<i>Ophoronid</i>	Sponge, SP22	Worm, Tube or Anemone, I04
<i>Oxysmilia rotundifolia</i>	Sponge, SP23	Worm, Tube or Anemone, I05
	Sponge, SP25	Worm, Tube or Anemone, I06
P	Sponge, SP32	Worm, Tube or Anemone, I07
<i>Padina</i> sp.	Sponge, SP34	Worm, Tube or Anemone, I09
<i>Petrosia</i> sp.	Sponge, SP35	Worm, Tube or Anemone, I11
<i>Placosporastra antillensis</i>	Sponge, white glass	Worm, Tube or Anemone, I12
<i>Pleraplysilla</i> sp.	Sponge, yellow ball glass	Worm, Tube or Anemone, I15
<i>Plesionika longicauda</i>	<i>Stenopus hispidus</i>	
<i>Plumapathes pennacea</i>	<i>Stylocidaris affinis</i>	Y
<i>Pseudoceratina crassa</i>	<i>Swiftia</i> sp.	<i>Yucatania sphaeroidocladus</i>
R	T	Z
<i>Rhizaxinella clava</i>	<i>Telmatactis</i> sp.	Zoanthid, mushroom
	<i>Thelogorgia gracilis</i>	
S	<i>Thelogorgia stellata</i>	Species Group 2
<i>Sargassum hystrix</i>	<i>Thesia rubra</i>	A
Sea biscuit	<i>Tosia parva</i>	<i>Agelas</i> cf. <i>cerebrum</i>
Sea Cucumber, CU1	Tunicate, T1	<i>Ancorina</i> sp.
Sea Cucumber, CU6	Tunicate, T2	Antipatharian, A05
Sea pen	Tunicate, T4	Antipatharian, A09
Sea star (UNK)	Tunicate, T5	Antipatharian, A13

Species or ID Code	Species or ID Code	Species or ID Code
Antipatharian, A15	W	T
	Worm, Tube or Anemone, I08	Tunicate, T12
E		
Echinoderm, ST07	Z	W
	Zoanthid	Worm, Tube or Anemone, I10
G		Worm, Tube or Anemone, I14
Gorgonian, G01	Species Group 3	
Gorgonian, G02	A	Species Group 4
	Algae, AL03	A
H	Antipatharian, A04	<i>Acanthella cubensis</i>
<i>Higginsia coralloides</i>	<i>Axinella waltonsmithi</i>	Algae, AL04
Hydroid, DFH8-6A		Algae, AL10
Hydroid, H03	C	Algae, AL13
Hydroid, H05	<i>Caulerpa</i> sp.	Algae, green
Hydroid, H10	Coral, Stony, S06	Algae, silted macro-
Hydroid, H11	Coral, Stony, S10	Antipatharian, A14
Hydroid, H15		<i>Aphanopathes pedata</i>
	D	Axinellidae
I	Dive 11196 sp.	
<i>Isostichopus badionotus</i>		B
	E	<i>Bebryce</i> sp.
M	Echinoderm, ST01	<i>Beggiatoa</i> sp.
<i>Muricia pendula</i>	Echinoderm, ST11	
		C
P	H	<i>Caliacis</i> sp.
Phoronid, Dive 22090	Hydroid, DFH8-11A	<i>Calligorgia gracilis</i>
<i>Placogorgia</i> sp.		<i>Chironephytha caribaea</i>
	M	<i>Cliona</i> sp.
S	<i>Microdictyon</i> sp.	Coral, Stony, S01
Sponge, SP02	<i>Montastraea cavernosa</i>	Coral, Stony, S03
Sponge, SP09		Coral, Stony, S08
Sponge, SP12	P	Crab, hermit
Sponge, SP17	<i>Plakortis zyggompha</i>	Crinoid
Sponge, SP27		Crinoid, CR04
Sponge, SP30	S	Crinoid, CR07
	Sponge, glass vase	Crinoid, CR12
V	Sponge, SP33	<i>Crinometra brevipinna</i>
<i>Verongula reiswigi</i>		

Species or ID Code	Species or ID Code
E	W
<i>Ellisella</i> sp.	Worm, Tube
	Worm, Tube or Anemone, I02
G	
Gorgonian, UnID	
H	
<i>Haliclona</i> sp.	
<i>Halimeda goreau</i>	
Hydroid, DFH8-18B	
Hydroid, H12	
I	
<i>Ircinia</i> sp.	
L	
<i>Lysmata grabhami</i>	
M	
<i>Madracis cf. asperula</i>	
<i>Muriceides</i> sp. cf. <i>furta</i>	
<i>Muricia</i> sp.cf. <i>furta</i>	
N	
<i>Neopetrosia</i> sp.	
P	
<i>Phanopathes expansa</i>	
S	
<i>Sargassum</i> sp.	
<i>Scleracis</i> sp.	
Sp. 1, UnID	
Sponge, cupped	
Sponge, Encrusting blue	
Sponge, SP21	
Sponge, SP26	
Sponge, UnID	
Sponge, yellow glass vase	

All species in Species Group #1 had abundance proportions of ≤ 0.20 . This included *Diodogorgia nodulifera*, *Thelogorgia gracilis*, *Plumpathes pennacea*, *Ventricria ventricosa*, and *Myrmikioderma gyroderma* densities (Table 9). (There are many as yet unidentified species which fall into this group as well.) As mentioned above, groups of biota included taxa identified down to species and others down to only genus, class, order, etc. This approach, which is necessitated by the photographic sampling technique, most likely makes these results more conservative than otherwise. We are not aware of any entries where phenotypic morphological variants of the same species have been entered as multiple entries for the same species.

Species Group #2, on the other hand, is home to several species with high abundances. These have high impacts on determining the assignment of banks to Bank Groupings, which is based solely on species composition and comparative abundances (Table 8). The names of the major species contributing to Group #2, and having a major influence on several Bank Groups, are presented in enlarged type and/or bold in Table 8. An example of species with an abundance impact factor of 1.0 is *Antipathes* sp. particularly impacting Sonnier Reef, and Gorgonian G04, impacting Bouma Reef at 0.81-0.99. The vast majority of species, identified or unidentified, within this Species Group have less than 0.20 comparative abundances (Table 9). This includes *Muricea pendula*, *Higginsia coralloides*, *Placogorgia* sp., and *Agelas* cf. *cerebrum*. Most of the species in this Species Group are as yet unidentified.

Species Group #3 contains a small number of species, and all have an abundance ranking of ≤ 0.20 . This is similar to Species Group #1 (Table 9). This would include *Montastraea cavernosa*, *Axinella waltonsmithii*, *Caulerpa* sp., *Plakortis zygompha*, and *Microdictyon* sp. Most of the other species are yet to be identified. Here, there were no species which reached a measurable abundance impact.

Species Group #4 is by far the Group with the greatest number of species and the highest comparative abundances (Table 8). This included Sea Fan and *Stichopathes* sp., impacting 29 Fathom Reef in Bank Group #1 most heavily. 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. *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 also dominated Rezak Bank as well as Elvers, McGrail, and Sidner Banks, forcing these Banks into Bank Group #3. Algae AL-12 UnID was accompanied by a red encrusting sponge in helping to characterize Elvers Bank and assign it to Bank Group #3. Rankin Bank was characterized primarily by pink and red encrusting sponges, also helping to force 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 Bank Group #2. Those species with lowest comparative abundances in Species Group #4 included *Muricea* sp. cf. *furta*, *Aphanipathes pedata*, *Acanthella cubensis*, *Ircinia* sp., *Chironephytha caribaea*, and *Madracis* cf. *asperula* (Table 9).

Table 10 presents a collation of only the five most abundant sessile epibenthic species occurring on each bank. Ten of the banks surveyed fell into Bank Group #3 and are characterized by high species abundances. These included *Nicella* sp., *Elatopathes abientina* (two color morphs), and unidentified pink and red encrusting sponges. This Bank Group (#3) also exhibits a high level of species richness, ranging from 117 to 207 species per bank. Composition of the five most abundant species within Bank Group #3 varied greatly between banks. Horseshoe, 28 Fathom, and Bright Banks possessed similar dominant species. The remainder of the banks in Bank Group #3 were characterized by *Peysonellia* sp., yellow and orange encrusting sponges, unID algae #12, and a red encrusting sponge. 29 Fathom and Sonnier Banks (Bank Group #1), on the other hand, overlapped in comparative abundance in only two of the five most abundant species within its Bank Group. These taxa were a sea-fan shaped antipatharian and a bryozoan-like tubeworm. Both of these banks, however, exhibited low species richness in comparison to the 10 banks in Bank Group #3. The species richness on 29 Fathom Bank is particularly low, being only 56 species.

Table 10. Abundances in terms of colony counts of the most abundant five species or taxa.

Shown for the 13 study banks. Banks presented by Bank Grouping, determined by PATN[©]. Total number of species or taxa also shown for each bank.

Group:	Bank										2		1	
	Horseshoe	28 Fathom	Bright	Alderdice	Bouma	Rankin	Rezak	Elvers	McGrail	Sidner	Geyer	29 Fathom	Sonnier	
<i>Nicella</i> sp.	510.05	310.25	414.7						570.7	364.4				
<i>Elatopathes abientina</i> (white)	256.75	331.45	229.85											
<i>Elatopathes abientina</i> (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	
<i>Stichopathes</i> 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						
<i>Peysonellia</i> sp.			586.5					596.2	428.3	537.75	1,343.40			
<i>Tanacetipathes</i> sp.			205.35											
Turf Algae											994.2			
Hydroids				281.4					635.9	534.25	560.8			
<i>Beggiatoa</i> sp.											163.5			
<i>Antipathes furcata</i>				225.5					533.9					
<i>Antipathes</i> sp.													1,216.55	
DFH8-16B													305.8	
G04													116.6	
Verdigellos								909						
AL04									498.9					
Total No. Species	174	168	117	134	140	207	146	157	128	132	89	56	116	
& Taxa per Bank														

Geyer Bank exhibited its own dominant species patterns, including *Peysonnelia* sp., turf algae, and hydroids as its most abundant taxa. The species richness on Geyer Bank was also particularly low in comparison to almost all other banks; it was the second lowest number, at 89 species.

3.2.5 Box-and-Whisker Results

The Box-and-Whisker diagrams indicate which sessile epibenthic Species Groups, discussed above, best characterize a particular bank and to what extent. 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.

From this diagram, one can discern that, Bouma Bank is well differentiated from all other banks within Bank Group #3, driven by the distribution and abundances of the fauna and flora in Species Group #4 and also Species Group #2 (Fig. 20). 28 Fathom Bank mimics this pattern to some degree. The remainder of the banks within Bank Group #3 possesses very similar profiles in Species Groups; i.e., Species Group #4 made the largest contribution to the characterization of this set of banks, with the additional influence of Species Group #2.

Bank Group	Species Bank	Species Group	Species Group	Box-and-Whisker Values		
Number	Number	Means	0%	50%	100%	
3	Horsehoe	1	0.76	0	255	510
		2	1.04	0		
		3	0.022	0		
		4	36.9	0		
	28 Fathom	1	0.92	0	166	331
		2	2.09	0		
		3	0.011	0		
		4	41.1	0		
	Bright	1	0.85	0	293	587
		2	2.55	0		
		3	0.042	0		
		4	45.1	0		
Alderdice	1	1.54	0	181	362	
	2	1.42	0			
	3	0	0			
	4	34.2	0			
Bouma	1	0.89	0	105	209	
	2	4.22	0			
	3	0	0			
	4	34.3	0			
Rankin	1	2	0	835	1,670	
	2	1.89	0			
	3	0.69	0			
	4	113	0			
Rezak	1	0.9	0	853	1,706	
	2	1.35	0			
	3	0.14	0			
	4	83.5	0			
Elvers	1	1.42	0	1,007	2,014	
	2	0.72	0			
	3	0.011	0			
	4	115	0			
McGrail	1	0.91	0	1,599	3,199	
	2	0.18	0			
	3	0.05	0			
	4	114	0			
Sidner	1	0.68	0	1,439	2,878	
	2	0.62	0			
	3	0.12	0			
	4	89.4	0			
2	Geyer	1	0.31	0	672	1,343
		2	0.17	0		
		3	0.017	0		
		4	52.1	0		
1	29 Fathom	1	0.15	0	113	227
		2	11.9	0		
		3	0.014	0		
		4	8.89	0		
	Sonnier	1	0.69	0	608	1,217
		2	61.7	0		
		3	0	0		
		4	9.76	0		

Figure 20. Box-and-Whisker diagrams (Sokal and Rohlf, 1981) showing sessile epibenthic Species Groups that best characterize a bank.

Box size is an indicator of degree of contribution, denoting the inner two quartiles of the abundances in that group, i.e., 25–75%. Whiskers indicate the range of values in that Species Group. Values for individual Species Groups are shown and indicate the strength of each Species Group in discriminating between one Bank Group and another. For each Species Group, the far-left end of the line represents the minimum value in that Group. The far-right end of the line represents the maximum value of the range for that Species Group. The “x” represents the mean. The scale along the top of each row represents the range of abundances for that species group, delineating the 0%, 50%, and 100% values of abundance.

Bank Group #1 contains 29 Fathom and Sonnier Banks. There, Species Group #2 had the strongest presence and influence on bank characterization, with a secondary influence by Species Group #4. 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 on this bank.

3.2.6 Special Designations for Taxa Encountered

It is of interest to identify any special designations for taxa encountered in this study, particularly since these banks have not been surveyed at these depths and this extensively before this study. This includes information on any new species or extended distributions of taxa encountered, or the occurrence of rare, threatened, endangered, endemic, or protected species. Due to the large number of taxa encountered and the lack of detailed information available on these groups (most taxa could not be identified down to species), however, it is beyond the scope of this study to define such in detail.

Nonetheless, one group which has received particular attention during the study, primarily due to the training and experience of the investigators, is the Cnidaria. We have included what information is known on their geographic range; whether they are endemic; and whether they are listed by the US National Marine Fisheries Service (NMFS), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), or International Union for the Conservation of Nature (IUCN) Red List as protected or endangered species. Information is also included on whether they have received any protection in local Marine Protected Areas (MPAs). Designations for these taxonomic groups may be found in Table 11. Designations for the remainder of species in other phyla (those which were identified down to species) may be found in Table 12, with similar information which could be found for them. Regarding geographic range extensions, any organism listed by its full genus and species name in either of these tables may now be considered to also be found in the Gulf, if such has not been logged in earlier reports.

Table 11. Table indicating special designations for cnidarian taxa encountered during this study.

Data include major taxonomic group and species name or code. Documented geographic range is also presented. Codes: GMx: Gulf of Mexico; C: Caribbean; Ba: Bahamas; SA: South Atlantic; EA: East Atlantic; SEFLA: Southeast Florida; BE: Bermuda; SEUS: Southeast US; WA: Western Atlantic; NEUS: Northeast US. Information also provided on endemism, as well as listings as protected or endangered species by NMFS, CITES, and the IUCN Red List.

Family	Species/Taxon	Geographic Range (Felder and Camp, 2009)	Endemic	Protection			
				National Marine Fisheries Service (NMFS) Protected Species List	CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora)	International Union for Conservation of Nature (IUCN) Red List	
Agariciidae	<i>Agaricia</i> sp.	SEFLA, Ba, C, Be, SA		No	No	Data Insufficient, to Vulnerable	
Caryophyllidae	<i>Oxymilla rotundifolia</i>	C, SA		No	Yes	Not Assessed	
	Colonial Cup Coral				Yes		
	Solitary Cup Coral				Yes		
Faviidae	<i>Montastraea cavernosa</i>	EA, Be, SEFLA, Ba, C, SA		No	Yes	Least Concern	
Oculinidae	<i>Madrepora carolina</i>	SEFLA, SEUS, Be, C		No	Yes	Not Assessed	
	<i>Oculina</i>	Be, SEFLA, Ba, C, GMx, SEUS		No	Yes	Data Insufficient, to Vulnerable	
	S02				Yes		
	S03				Yes		
	S08				Yes		
Pocilloporidae	<i>Madracis brueggemanni</i>	C, SA		No	Yes	Not Assessed	
	<i>Madracis</i> cf. <i>asperula</i>	EA, C, SA		No	Yes	Not Assessed	
	S01				Yes		
	S04				Yes		
	S06				Yes		
	S07				Yes		
	S09				Yes		
	S10				Yes		
	Alcyoniidae	<i>Anthomastus robustus</i>	GMx	to GMx	No	No	Not Assessed
Antipathidae	A01				Yes		
	A02				Yes		
	A03				Yes		
	A04				Yes		
	A05				Yes		
	A06				Yes		
	A15				Yes		
	Sea Fan				Yes		
	Sea Whip				Yes		
	<i>Antipathes furcata</i>	C, Ba, SA, EA		No	Yes	Not Assessed	
		Bermuda, Caribb, E Atl,					
		Europ Coasts, GMx					
	<i>Antipathes</i> sp.			No	Yes	Not Assessed	
	<i>Stichopathes</i> sp.	C, Ba, SA		No	Yes	Not Assessed	
Aphanipathidae	A07				Yes		
	A08				Yes		
	A09				Yes		
	A10				Yes		
	A11				Yes		
	A12				Yes		
	A13				Yes		
	<i>Acanthopathes thyooides</i>	C		No	Yes	Not Assessed	
	<i>Aphanipathes pedata</i>	C		No	Yes	Not Assessed	
	<i>Elatopathes abietina</i>	C		No	Yes	Not Assessed	
	<i>Phanopathes expansa</i>	GMx	to GMx	No	Yes	Not Assessed	
	Ellisellidae	A14					
		DFH8-6A					
DFH8-10A							
DFH8-11A							
<i>Ellisella</i> sp. (<i>Ctenocella</i> spp.)		Ba		No	No	Not Assessed	
G09							
<i>Nicella</i> sp.	EA, SEUS, C		No	No	Not Assessed		
Gorgoniidae	<i>Leptogorgia</i> sp.	GMx, SEUS, SA, NEUS, C		No	No	Not Assessed	
Keroeidae	G05			No	No	Not Assessed	
	<i>Thelogorgia stellata</i>	WA		No	No	Not Assessed	
	<i>Thelogorgia gracilis</i>						
Myriopathidae	<i>Plumapathes pennacea</i>	C, Ba, SA		No	Yes	Not Assessed	
	<i>Tanacetipathes</i> sp.	C, Ba, SA		No	Yes	Not Assessed	
Anthothelidae	<i>Diadogorgia nadullifera</i>	SEUS, C, SA		No	No	Not Assessed	
Nidaliidae	<i>Chironexphyia caribaea</i>	C		No	No	Not Assessed	
Plexauridae	<i>Bebryce</i> sp.	Ba, C		No	No	Not Assessed	
	<i>Calicis</i> sp.	C		No	No	Not Assessed	
	DFH8-18B				No		
	DFH11-12A				No		
	DFH11-21A				No		
	G01				No		
	G02				No		
	G03				No		
	G04				No		
	G06				No		
	G07				No		
	G08				No		
	G10				No		
	G11				No		
	G12				No		
	G13				No		
	G14				No		
	G15				No		
	<i>Hypnogorgia</i> sp.	C		No	No	Not Assessed	
	<i>Muricea pendula</i>	SEUS		No	No	Not Assessed	
<i>Muricea</i> sp.	C, EA, NEUS		No	No	Not Assessed		
<i>Placogorgia</i> sp.	C, SA, GMx		No	No	Not Assessed		
<i>Scleractis</i> sp.	C		No	No	Not Assessed		
<i>Swiftia</i> sp.	SEUS, C		No	No	Not Assessed		
<i>Thesea rubra</i>	C		No	No	Not Assessed		
Primnoidae	<i>Callogorgia gracilis</i>	Ba, C		No	No	Not Assessed	
Zoanthidae	Zoanthid				No		

Table 12. Table indicating special designations for all taxa except the Cnidaria encountered during this study.

(See Table 11 for data on Cnidaria.) Data include major taxonomic group; species name or code; geographic range; listings as protected or endangered species by CITES or inclusion in the IUCN Red List. No endemic species were encountered here. Also, no species were found to be listed on the NMFS protected list.

Taxonomic Group	Species/Taxon	Geographic Range[1]	Protection		
			CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora)	International Union for Conservation of Nature (IUCN) Red List	Other Protection (incl. local)
Porifera	<i>Corallistes typus</i>	Brazil, Florid, E. Caribb, S Caribb		Data Insufficient, to Vulnerable	
		N GMx			
	<i>Apiysilla suffurea</i>	Atl & Pacif			
	<i>Auleta sycularia</i>	Azores, Bermuda, FL			
	<i>Batzella rubra</i>	Greater antilles			
	<i>Ectoplysia ferox</i>	W. Atl, Caribb, GMx, Brazil			
	<i>Erylus alleni</i>	Caribb			
	<i>Erylus trisphaera</i>	FL, N GMx			
	<i>Myrmekioderma gyroderma</i>	Bahamas, Colombia			
	<i>Niphates erecta</i>	Bermuda, Bahamas, Caribb			
	<i>Pseudoceratina crassa</i>	Bahamas, Bermuda, E Caribb,			
		Gr. Antilles, S Caribb, SW Caribb			
		FL, Amazonia			
	<i>Rhizaxinella clava</i>	FL, GMx			
	<i>Yucatania sphaeroidocladus</i>	GMx, Mx			
	<i>Agelas cf. cerebrum</i>	Bahamas, Gr Antilles			
	<i>Higginsia coralloides</i>	Bahamas, Colombia, Grenada			
		GMx			
	<i>Verongula reisiwigi</i>	Cuba, Panama, Belize			
		Bahamas, Martinique			
	Caribb				
<i>Axinella waltonsmithi</i>	N GMx, Floridian, Carolinian				
<i>Plakortis zygompha</i>	Caribb, N GMx, Puer Rico,				
	Jamaica				
<i>Acanthella cubensis</i>	N GMx, Carolinian, Floridian,				
	S Caribb, SW Caribb				
Echinodermata	<i>Comactinia meridionalis</i>	GMx	Not evaluated		
	<i>Coronaster briareus</i>	W Atl			
	<i>Hacelia superba</i>	S Caribb, Jamaica - Nicaragua			
	<i>Stylocidaris affinis</i>	NC - Caribb, Bermuda,			
		Medditerr			
	<i>Isostichopus badiionatus</i>	W Atl, N Carol, Brazil, Caribb,			Bermuda
		West-Centr Africa,			
	N Pacif coast - S. Amer,				
	Galapagos Isl, N Venezuela				
<i>Crinometra brevipinna</i>	W Atl, E Atl, Caribb, Brazil, FL			Local MPA	
	Cuba				
Echinasteridae	<i>Henricia sexradiata</i>				
Cephalopoda	<i>Cyphoma gibbosum</i>	FL, Caribb, Brazil		No	
Gorgonacea	<i>Diadogorgia nodlifera</i>	W Atl, S FL, Bahamas, Caribb	Not evaluated		
Crustacea	<i>Mithrax hispidus</i>	Bermuda, St. Thomas			
	<i>Plesionika longicauda</i>	FL, GMx, Mx, Venezu			
	<i>Stenopus hispidus</i>	Pantropical, GMx			
	<i>Lysmata grabhami</i>	GMx, N Atl, Bermuda			
		Am Coasts, W Atl, Cape Verde,			
		Annobon, N Atl, Eur Waters,			
		Madeira, Red Sea			
	New Caledonia, Ascension Isl				
Algae	<i>Halymenia hancockii</i>	FL, Virg Isl, Panama, Colombia			
	<i>Sargassum hystrix</i>	FL, Caribb, GMx, Atl Isl's,			
		Philippines			
	<i>Ventricaria ventricosa</i>	FL, Caribb, Gmx, Atl Isl's, W Afr,			Local MPA
		Indian Oc Isl's, India, SW Asia,			
		Japan, N&W Austral, PNG,			
		Trop Pacif Isl's, Chile, GMx			
	<i>Halimeda goreau</i>	Belize, Caribb, Cuba, Panama			
		Singapore, Jamaica,			
	No endemic species				
	No Nat. Mar. Fish. Serv. (NMFS)				
	Protected Species				

[1]
 Encyclopedia of Life, 2016
 Felder and Camp, 2009
 NOAA Flower Garden Banks National Marine Sanctuary, 2016
 Smithsonian Tropical Research Inst., 2016
 World Porifera Database, 2016
 World Register of Marine Species, 2016
 Wikipedia, 2016

3.2.7 Percent-Cover of Sessile Epibenthic Taxa

Percent-cover of sessile epibenthic taxa were highly variable between banks (Table 13). This was evident at both the drop-site and bank level. Estimates of percent live cover on the banks were highly significantly different from each other ($p < 0.001$, RxC frequency analysis, G-test). The bank with the highest percent-cover of sessile epibenthic organisms was Rankin, with 26% cover. The lowest cover was found at Sonnier Bank, with 7%. The SDs around these means were relatively consistent, ranging from 2.5% to 8.4%. Percent live cover at individual drop-sites, when considered among all of the banks, ranged from 3.3% to 36.0%.

Table 13. Percent live cover of sessile epibenthic fauna and flora inhabiting the flanks of mesophotic banks in the northern Gulf at and near the edge of the continental shelf.

Data presented for individual drop-sites within banks. Summary percent-cover data also presented along with SD for each individual bank. Estimates of live percent cover on the banks are highly significantly different from each other ($p < 0.001$, RxC Frequency Analysis, G-test).

Percent-Cover by Drop-Site									Percent Cover by Bank		
Bank	Drop-Site	Percent Live Cover	Bank	Drop-Site	Percent Live Cover	Bank	Drop-Site	Percent Live Cover	Bank	Percent Live Cover	Standard Deviation
28 Fathom	1	6.92	Elvers	1	21.09	Rankin	1	24.55	Rankin	26.51	3.459
	2	5.53		2	35.19		2	23.36	Elvers	25.37	8.353
	3	9.42		4	33.04		3	27.35	McGrail	21.41	7.008
	4	6.49		5	23.06		4	31.42	Rezak	17.64	4.245
	5	8.70		6	31.17		5	22.19	Sidner	15.83	8.224
	6	5.18		7	25.42		6	32.05	Bouma	12.20	3.545
	7	5.14		8	35.99		7	24.23	Geyer	12.05	4.119
	8	3.77		9	11.82		8	22.88	Alderdice	11.29	2.793
	9	5.58		10	12.17		9	28.71	Horseshoe	8.88	3.256
	10	4.18		11	21.43		10	29.45	28 Fathom	7.78	5.577
		11		24.62							Bright
29 Fathom	1	4.43	Geyer	1	19.45	Rezak	1	23.58	29 Fathom	7.30	2.448
	2	3.81		2	4.75		2	16.51	Sonnier	6.92	2.259
	3	2.83		3	7.23		3	14.87			
	4	9.58		4	13.94		4	17.79			
	5	9.98		5	9.25		5	22.80			
	6	8.79		6	16.24		6	14.87			
	7	9.00		7	10.17		7	13.32			
	8	5.26		8	12.34		8	12.14			
	9	7.25		9	14.46		9	24.71			
	10	7.41		10	12.12		10	15.94			
Alderdice	1	8.34	Horseshoe	1	8.49	Sidner	1	23.06			
	2	9.78		2	7.61		2	28.05			
	3	10.77		3	7.40		3	9.40			
	4	12.16		4	9.67		4	11.04			
	5	12.24		5	12.29		5	6.39			
	6	11.35		6	6.26		6	19.83			
	7	12.91		7	9.05		7	27.71			
	8	16.79		8	18.34		8	18.74			
	9	5.85		9	9.83		9	7.05			
	10	12.91		10	8.59		10	6.97			
Bouma	1	12.25	McGrail	1	19.23	Sonnier	1	5.33			
	2	11.11		2	25.21		2	4.86			
	3	16.14		3	35.52		3	6.68			
	4	19.82		4	9.35		4	8.43			
	6	8.86		5	28.07		5	5.58			
	7	8.02		6	23.11		6	11.80			
	8	13.70		7	15.09		7	3.26			
	9a	11.17		8	15.40		8	8.06			
	9b	8.28		9	19.30		9	6.08			
	10	10.14		10	21.65		10	7.94			
Bright	1	5.75									
	2	8.48									
	3	6.59									
	4	3.71									
	5	12.13									
	6	7.35									
	7	12.74									
	8	7.70									
	9	5.66									
	10	4.68									

3.2.8 Relationship between Mean Relief and Percent Cover

When percent live cover of sessile epibenthic fauna and flora were considered as a function of relief on the individual banks, a strong positive correlation was found. Percent-cover of epibiota clearly increased as relief increased on the banks (Fig. 21). The same relationship was found to occur when the relationship was considered at the drop-site level (Fig. 22).

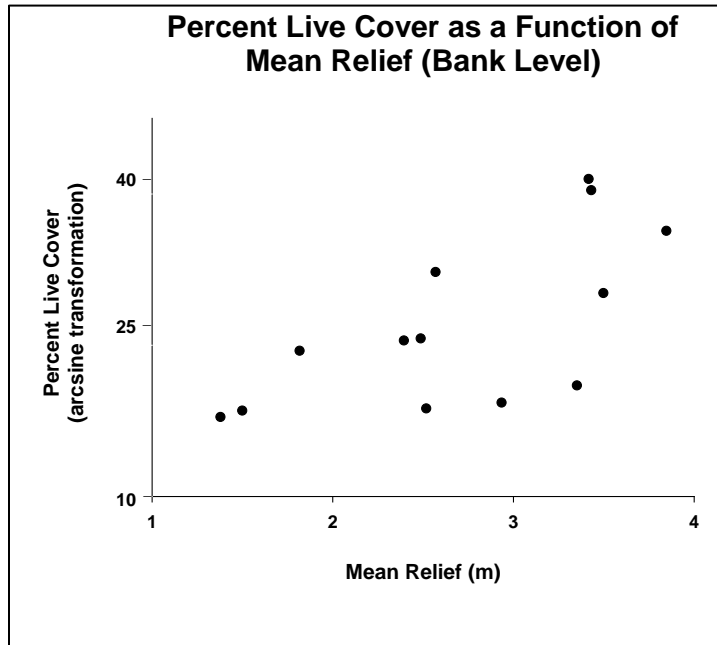


Figure 21. Graph: relationship between mean benthic relief on the study banks & percent live cover of the associated sessile epibenthic fauna and flora.

Percent-cover data have been transformed by arcsine for normalization purposes (Sokal and Rohlf, 1981). Percent-cover increases significantly with an increase in benthic relief ($r = 0.670$, Pearson's Product-Moment Correlation Analysis).

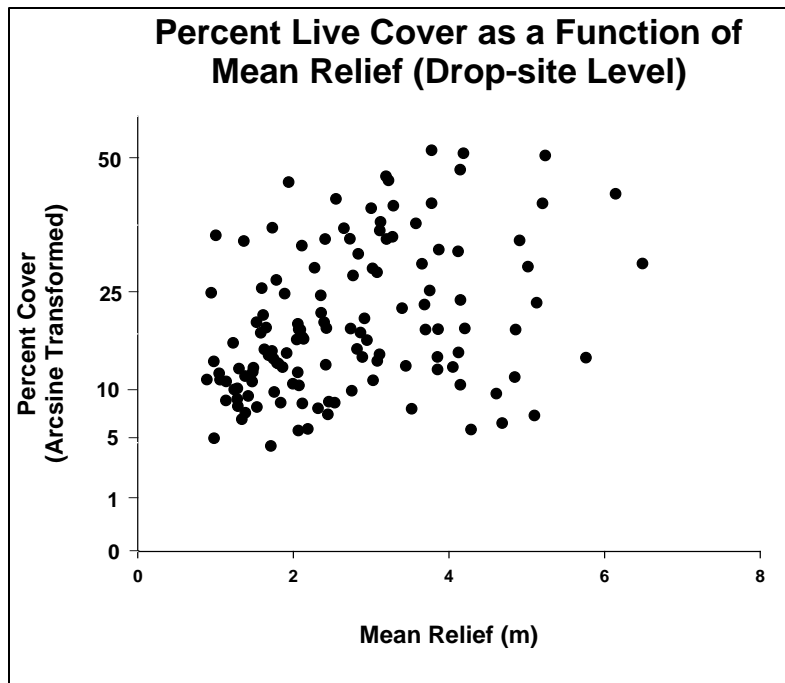


Figure 22. Graph: relationship between mean benthic relief on individual drop-sites & percent live cover of the associated sessile epibenthic fauna & flora.

Percent-cover data have been transformed by arcsine for normalization purposes (Sokal and Rohlf, 1981). Percent-cover increases significantly with an increase in benthic relief ($r = 0.363$, Pearson's Product-Moment Correlation Analysis).

3.2.9 Species Richness and Species Diversity

Species richness and species diversity was calculated for each drop-site, in order to obtain an understanding of the level of species richness for each bank and how it varied between banks. In addition, species diversity was calculated for each drop-site on each bank (pooling all transects within a drop-site) in order to gain an understanding of the amount of variability in richness between dropsites. It was also possible to examine the data for any within- and between-bank patterns which might co-vary with relief patterns. These data are summarized below in Table 14.

Table 14. All banks surveyed and their physical and biological characteristics.

Banks and drop-sites within banks are shown. Values of relief for each dropsite are shown as mean relief and SDR. Species diversity is shown as species richness (number of species, S), H' (Shannon-Wiener Species Diversity Index), and J' (Shannon-Wiener Species Equitability Index).

		Relief		Species Diversity					Relief		Species Diversity		
Bank	Drop-Site	Mean	StDev	No. Species (S)	H'	J'	Bank	Drop-Site	Mean	StDev	No. Species (S)	H'	J'
28 Fathom	1	2.073	0.8188	55	3.029	0.756	Horseshoe	1	4.0507	2.4188	81	2.955	0.673
	2	2.116	0.8953	50	2.914	0.745		2	4.8456	3.4011	79	3.098	0.709
	3	3.8527	1.7529	67	2.791	0.664		3	1.0577	0.4296	15	1.665	0.615
	4	2.7512	1.5579	54	2.726	0.683		4	3.1073	1.6674	75	3.278	0.759
	5	2.417	1.3328	152	3.563	0.709		5	2.4253	2.0227	63	2.954	0.713
	6	2.3173	1.0286	53	2.867	0.722		6	4.6083	3.1145	55	2.865	0.715
	7	3.5211	1.3225	58	2.850	0.702		7	3.0797	1.7674	49	2.997	0.770
	8	4.284	2.1102	55	3.028	0.756		8	2.7664	1.6508	66	3.113	0.743
	9	2.5315	1.0297	58	2.915	0.718		9	4.1221	2.4816	78	3.304	0.758
	10	4.6833	2.982	52	3.050	0.772		10	3.446	2.1498	75	3.209	0.743
	11	1.7306	0.6961	100	3.265	0.709							
29 Fathom	1	1.3383	0.489	13	2.041	0.796	McGrail	1	3.0181	1.3585	44	1.953	0.516
	2	2.1868	1.0131	14	2.100	0.796		2	3.5745	1.7122	65	2.419	0.579
	3	1.7104	0.6966	6	1.584	0.884		3	4.1863	2.0389	60	2.231	0.545
	4	1.6822	0.8518	14	1.723	0.653		4	5.7605	2.6735	53	2.265	0.571
	5	1.7254	0.9648	29	2.552	0.758		5	3.7771	2.0706	53	1.538	0.387
	6	1.8086	0.5472	18	2.286	0.791		6	2.727	1.0035	61	2.729	0.664
	7	0.9776	0.3936	7	1.680	0.863		7	5.127	2.3479	54	2.404	0.603
	8	1.5319	1.1033	33	2.912	0.833		8	4.1472	2.1201	57	2.305	0.570
	9	1.137	0.4388	16	2.206	0.796		9	2.2724	1.2271	52	2.396	0.606
	10	0.8886	0.5105	19	2.448	0.831		10	3.8694	1.8814	56	2.319	0.576
Alderdice	1	1.3016	0.4502	43	2.984	0.793	Parker	1	1.5916	0.5004			
	2	1.9136	0.79	40	2.840	0.770		3	1.5979	0.5999			
	3	1.2262	0.4971	31	2.723	0.793		4	2.9773	1.5045			
	4	2.0701	0.8442	48	3.181	0.822		5	2.3445	0.9155			
	5	2.737	1.1821	49	2.974	0.764		6	1.8645	0.8174		no data	
	6	2.1154	0.8324	53	3.218	0.811		7	5.9987	3.003			
	7	2.3954	0.7844	46	3.070	0.802		8	1.6719	0.6549			
	8	1.5948	0.9364	67	2.854	0.679		9	1.6762	0.6827			
	9	1.2798	0.4399	36	2.813	0.785		10	2.4224	1.0934			
	10	1.5265	0.6712	54	2.788	0.699							
Bouma	1	4.2046	2.0678	66	2.935	0.701	Rankin	1	2.6506	1.5288	83	3.164	0.716
	2	2.0443	0.905	55	3.010	0.751		2	3.2736	1.7767	74	3.281	0.762
	3	1.8888	0.8797	72	3.111	0.727		3	3.0012	1.6284	103	2.574	0.555
	4	3.654	1.2283	71	3.549	0.832		4	3.2234	1.376	77	2.811	0.647
	6	1.7894	0.7076	49	3.063	0.787		5	2.1102	0.7944	83	2.404	0.544
	7	2.0573	0.7117	47	2.772	0.720		6	3.1917	1.5025	114	2.848	0.601
	8	1.6117	0.6452	75	3.477	0.805		7	3.1112	1.5064	103	2.812	0.607
	9a	2.1322	1.953	49	2.822	0.725		8	4.9079	2.9473	85	3.204	0.721
	9b	3.8533	1.9987	51	2.583	0.657		9	2.5473	0.8972	116	3.054	0.642
	10	1.6287	0.7804	54	2.850	0.714		10	6.1412	3.5731	119	3.282	0.687
Bright	1	1.1332	0.5295	45	3.050	0.801	Rezak	1	1.0038	0.3802	70	2.647	0.623
	2	1.8615	0.8266	55	2.414	0.602		2	3.7531	1.4466	61	2.863	0.697
	3	1.24	0.5708	47	2.963	0.770		3	3.6848	1.564	60	2.561	0.625
	4	2.0641	0.8594	34	2.619	0.743		4	1.781	0.7628	70	2.733	0.643
	5	4.856	2.5406	49	2.986	0.767		5	1.3636	0.6537	67	2.735	0.651
	6	3.0249	1.2682	44	3.032	0.801		6	no data	no data	60	2.768	0.676
	7	2.0579	0.9312	44	2.545	0.673		7	2.9139	1.3869	59	2.901	0.712
	8	1.3795	0.5883	27	1.541	0.468		8	3.6977	1.5104	60	2.561	0.625
	9	2.4575	1.1428	33	2.523	0.722		9	no data	no data	70	3.068	0.722
	10	5.0982	2.1375	50	3.217	0.822		10	2.3523	0.9482	50	2.301	0.588
Elvers	1	2.8337	1.1485	77	2.581	0.594	Sidner	1	3.1977	1.4129	31	1.481	0.431
	2	5.237	2.1429	67	3.102	0.738		2	5.2023	1.9623	48	1.668	0.431
	4	4.1445	2.605	80	2.587	0.590		3	2.8869	1.2221	24	2.085	0.656
	5	2.4084	1.1341	78	2.784	0.639		4	2.9466	1.2624	45	2.773	0.729
	6	1.9404	0.8291	73	2.508	0.585		5	1.7549	0.8224	36	2.562	0.715
	7	3.12	1.4538	63	2.287	0.552		6	6.4871	3.1807	40	1.963	0.532
	8	3.777	2.0146	56	2.009	0.499		7	3.2848	1.5324	65	2.211	0.530
	9	2.8627	1.2995	72	3.104	0.726		8	3.0758	1.7254	61	2.260	0.550
	10	3.8606	1.8011	35	1.893	0.532		9	1.995	0.9465	35	2.669	0.751
	11	4.117	1.3272	30	2.372	0.697		10	4.1461	2.5506	36	2.418	0.675
	Geyer	1	5.015	1.8376	36	1.746		0.487	Sonnier	1	1.2876	0.486	40
2		2.444	1.1756	28	1.977	0.593	2	1.3827		0.5094	34	2.452	0.695
3		1.4709	0.6107	36	2.809	0.784	3	1.281		0.4634	40	2.383	0.646
4		2.3574	1.2068	25	1.430	0.444	4	1.4875		0.4559	45	2.492	0.655
5		1.7452	0.8274	25	1.573	0.489	5	1.8381		0.5015	39	2.984	0.814
6		0.9453	0.4382	23	1.911	0.610	6	1.5816		0.7499	40	2.383	0.646
7		2.8185	1.1856	37	2.603	0.721	7	0.9808		0.3635	36	2.858	0.797
8		1.6509	0.8369	45	2.209	0.580	8	1.4791		0.71	51	2.091	0.532
9		3.3974	1.3341	36	1.746	0.487	9	1.4199		0.7095	34	2.246	0.637
10		2.091	0.9987	26	1.788	0.549	10	1.0472		0.4506	42	2.655	0.710

A statistical analysis of species richness between banks revealed a highly significant difference between banks, analyzing the data at the drop-site level ($p < 0.001$, one-way ANOVA). An *a posteriori* pair-wise comparison between individual banks also revealed which of those banks vary significantly from each other. These comparisons are summarized in Table 15.

Table 15. Results of an all pair-wise *a posteriori* comparisons test assessing differences among all banks for species richness.

(Number of species, S). T', T-K, and G2 tests were run. An asterisk designates a significant difference between two banks. All bank comparisons are shown.

Bank	Bank												
	Horseshoe	29 Fathom	28 Fathom	Rankin	Bright	Geyer	Elders	McGrail	Sonnier	Bouma	Rezrak	Sidner	Alderdice
Horseshoe			*	*	*	*	*	*	*	*	*	*	*
29 Fathom							*	*	*	*	*	*	*
28 Fathom										*	*	*	*
Rankin												*	*
Bright												*	*
Geyer												*	*
Elders													*
McGrail													*
Sonnier													*
Bouma													*
Rezrak													*
Sidner													*
Alderdice													*

These two analyses demonstrate that species richness is highly variable between banks. It also shows that it is highly variable within a given bank; that is, species richness is not necessarily predictable between banks, or in given sectors within a bank. It is possible, however, that species richness is in general linked to relief on the banks, and this will be addressed below. Regarding some specifics, one should recall that Horseshoe and 29 Fathom Banks had very low and predictable relief. Note here that these banks are also significantly different from most of the other banks with respect to their species richness. On the other hand, Sidner and Alderdice Banks were two of the banks with the highest relief. Here, we have found that they are also highly significantly different from their sister banks in species richness. These concepts will be examined in greater detail below.

3.2.10 *Habitat Characterization Based on Species Richness*

As noted above, the 13 banks surveyed differed in species richness. In addition, species richness varied between drop-sites, within a bank, revealing within-bank patterns of number of species. The banks fell into groups characterized by these patterns of species richness. 3-D graphing revealed that the largest set of banks (5) had peaks in species richness in the northwestern sector. These were 28 Fathom, 29 Fathom, Bright, McGrail, and Rankin Banks (Fig. 23). A similar set of banks, however, exhibited species richness peaks in the southwestern sector. These were Alderdice, Bouma, Geyer, and Sonnier Banks (Fig. 24). The last four banks each exhibited

patterns of species richness different from the previous two sets – and different from each other (Fig. 25). These were Elvers Bank, with a species richness peak in the north; Sidner Bank, with a peak in the northeast; Horseshoe Bank, with its peak in the east; and Rezak Bank, with its peak extending broadly from the southeast to the southwest. A review of these individual bank patterns placed into geographic context over the entire study area showed no overall discernible geographic pattern in patterns of species richness.

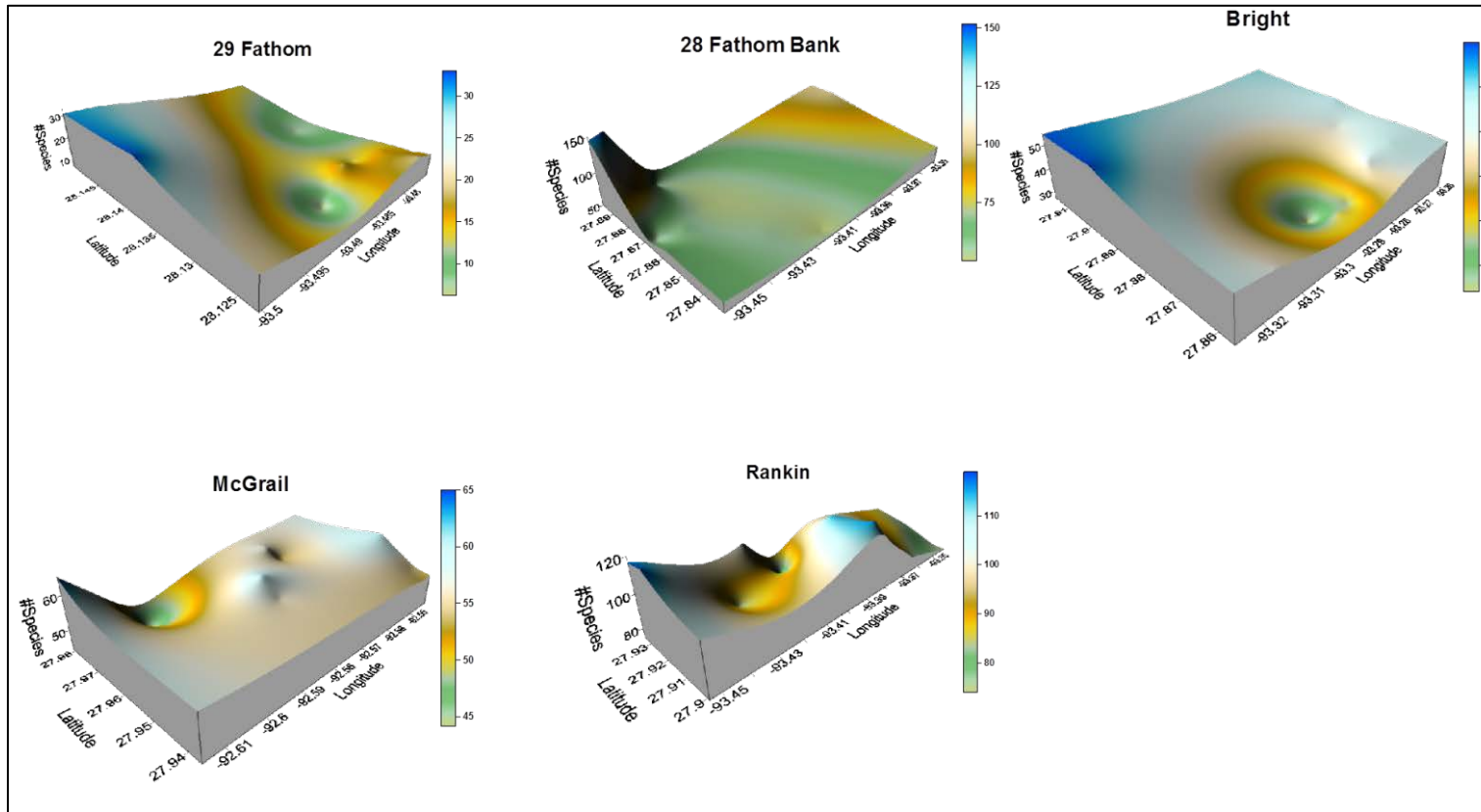


Figure 23. 3-D representation of the distribution of species richness of sessile, epibenthic fauna & flora on five banks. Banks: 29 Fathom, 28 Fathom, Bright, McGrail, and Rankin. North is at approximately 10:00 in all cases. All peaks are in the northeast.

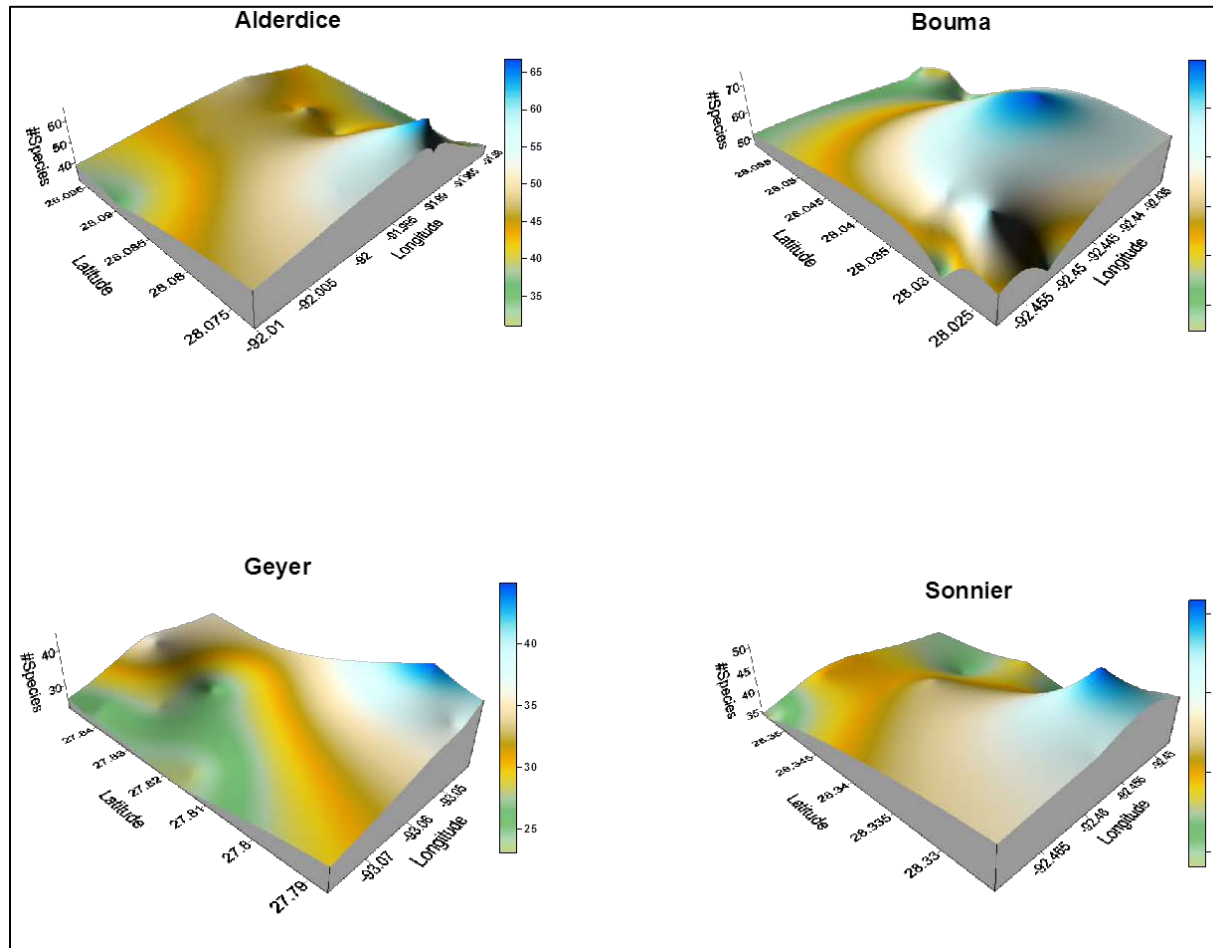


Figure 24. 3-D representation of the distribution of species richness of sessile, epibenthic fauna & flora on four banks. Banks: Alderdice, Bouma, Geyer, and Sonnier. North is at approximately 10:00 in all graphs. All peaks are in the southeast.

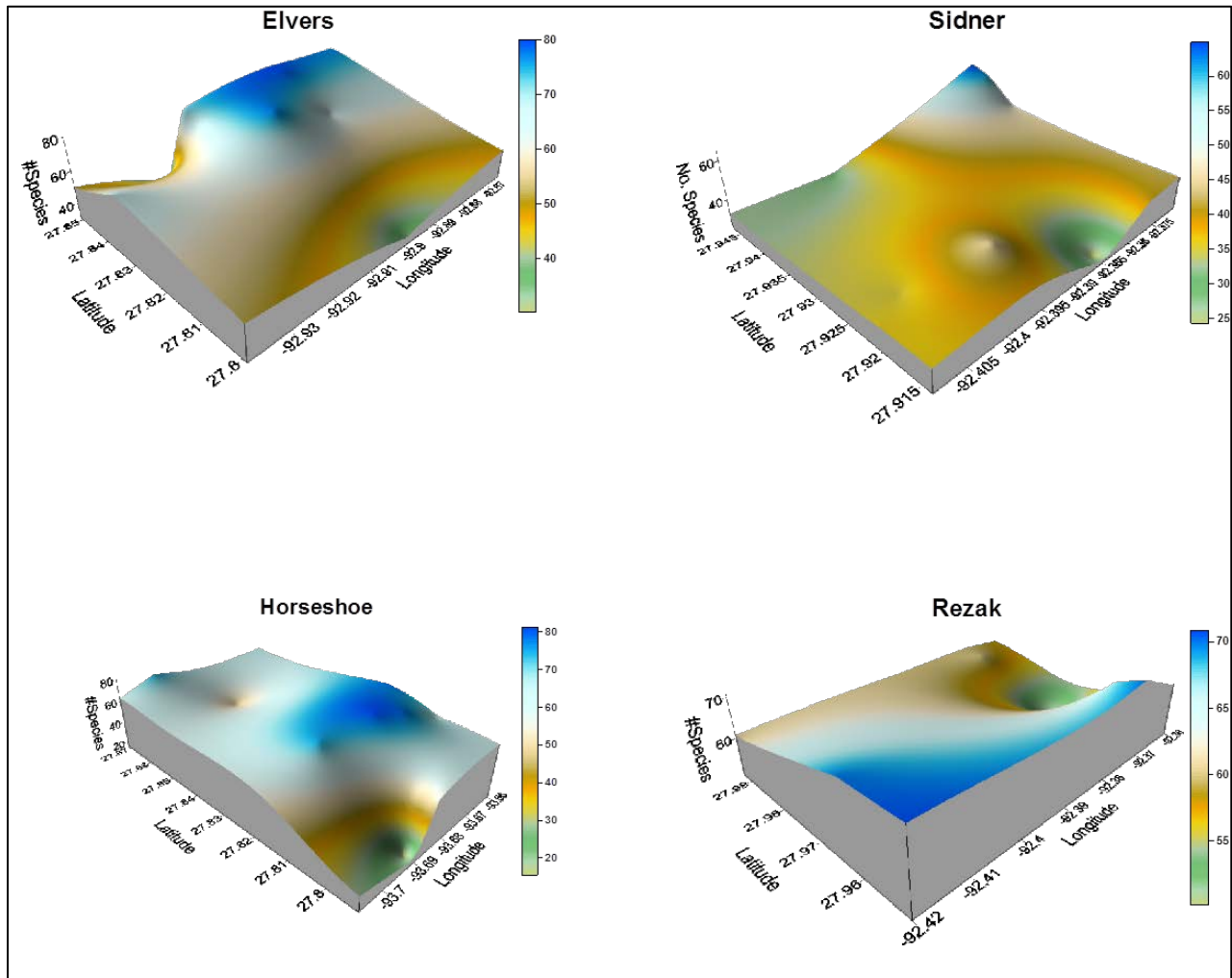


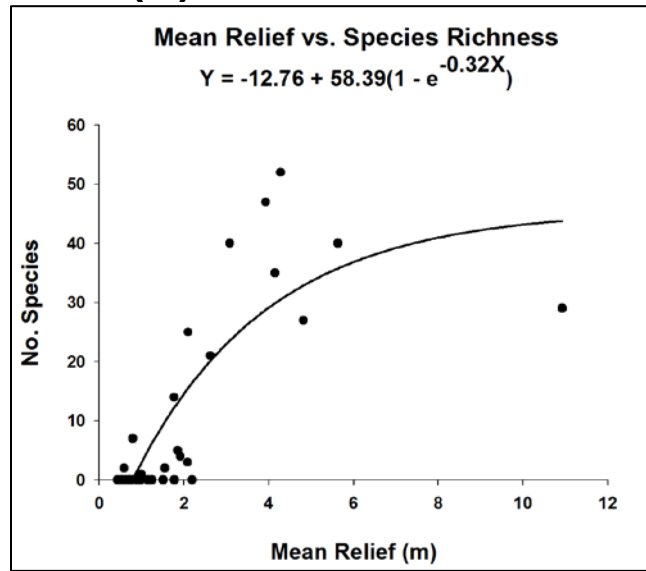
Figure 25. 3-D representation of the distribution of species richness of sessile, epibenthic fauna & flora on four banks. Banks: Elvers, Sidner, Horseshoe, and Rezak. North is at approximately 10:00 in all graphs. No peaks coincide; they are in the north, northwest, east, and southeast to southwest.

3.3 Relationship between Relief and Species Richness, including Geographic Patterns

3.3.1 Analysis of Preliminary Data: Two-way Analysis

In the first instance, as an analysis of preliminary data obtained early in the project, available transect data from three drop-sites derived from Horseshoe Bank were analyzed for a relationship between mean relief and species richness. Graphics and analyses revealed a positive relationship between the two variables, defined by an asymptotic curve (Fig. 26a; $r = 0.84$; $p < 0.001$). The curve was described by the following equation: $y = -12.76 + 583.39(1 - e^{-0.32X})$.

(A)



(B)

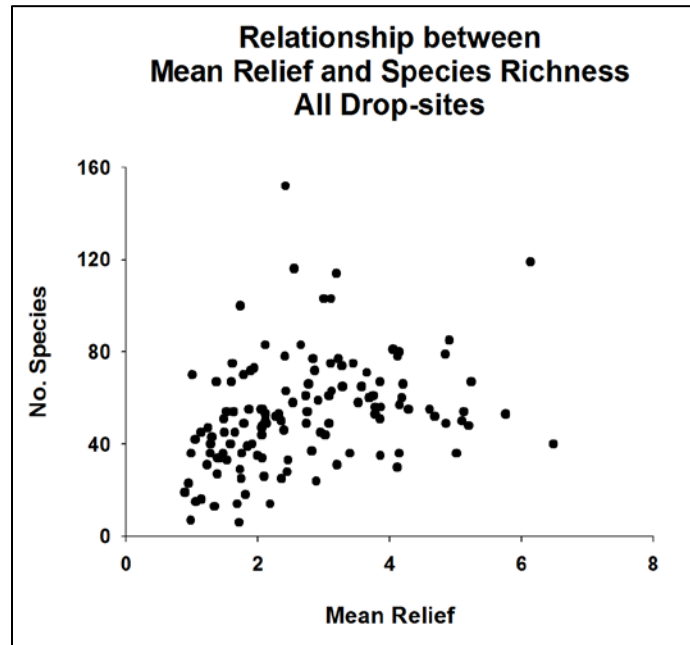


Figure 26. Graphs: relationship of mean relief on a bank & species richness and species richness as function of mean relief.

(A) Relationship between Mean Relief on a bank & species richness of the mesophotic sessile epibenthic community. Based on preliminary data drawn from Horseshoe Bank, Gulf of Mexico, encompassing 3-4 drop-sites or ~35 transects. Highly significant correlation ($p < 0.001$, $r =$

0.620, Pearson's product-moment correlation analysis) and highly significant asymptotic curve describing relationship ($y = -12.76 + 58.39[1 - e^{-0.32X}]$, $p < 0.001$). (B) Species richness as a function of mean relief, but at the drop-site level of spatial resolution. Data drawn from all drop-sites within all banks ($n = 129$). Highly significant correlation ($p < 0.001$, $r = 0.342$).

3.3.2 Analysis of Relief and Species Richness Data Sets: Two-way Analyses

When all data from the study were available, drop-site data were plotted against mean relief for the same banks. Again, a weaker but positive relationship was found with a significant correlation (Fig. 26b; $r = 0.34$, $p < 0.001$). There was much more variance in the relationship when all drop-sites from all banks were considered, but the relationship was still valid.

Considering this relationship at the bank level of resolution, it was clear that there was a significantly positive relationship between mean relief and species richness when all banks were considered together (Fig. 27; $r = 0.58$, $p < 0.05$; Model II Regression, $y = 48.40 + 30.85X$, $p < 0.05$). Despite the fact that there were relatively few points involved in the analysis ($n=13$, number of banks), yielding a low power of the test because of the number of banks sampled, this relationship was still significant and emerged clearly.

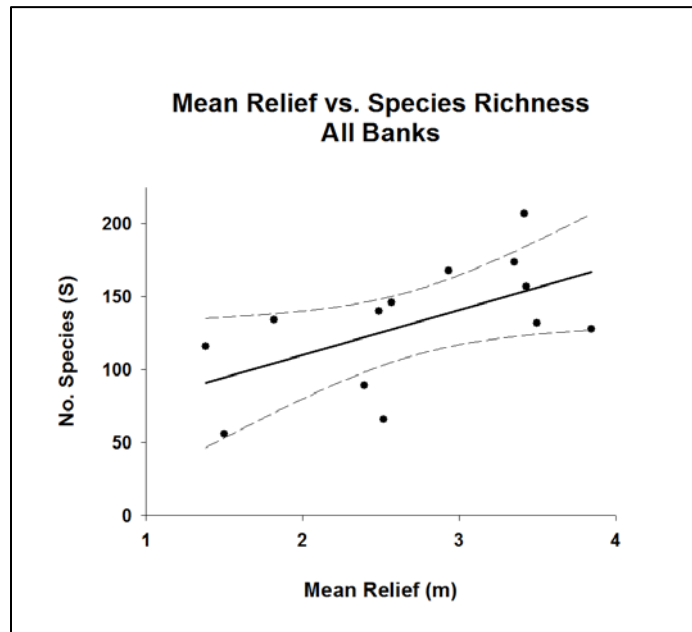
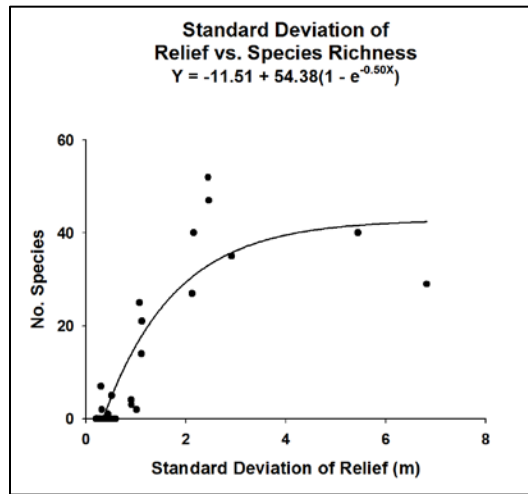


Figure 27. Graph: relationship between mean relief and species richness of the mesophotic sessile epibenthic community at the bank level of spatial resolution.

All 13 study banks in the Gulf shown. Significant correlation between the two variables ($r = 0.577$, $p < 0.05$, Pearson's product-moment correlation analysis). Also, significant positive Model II linear regression analysis ($p < 0.05$, $y = 48.40 + 30.85X$). 95% confidence bands also shown for regression line.

We also considered the relationship of the SDR against species richness. When considering the preliminary data from Horseshoe Bank, and when species richness was plotted against the SD of bottom relief, it became clear that, again, there was a highly significantly positive relationship between the two variables (Fig. 28a; $r = 0.74$, $p < 0.001$; $y = -11.51 + 54.38[1 - e^{-0.50x}]$, $p < 0.001$). A similar significantly positive relationship emerged when species richness was plotted against SDR for all drop-sites on all banks. There was a clear significantly positive correlation between the two variables (Fig. 28b; $r = 0.38$, $p < 0.001$).

(A)



(B)

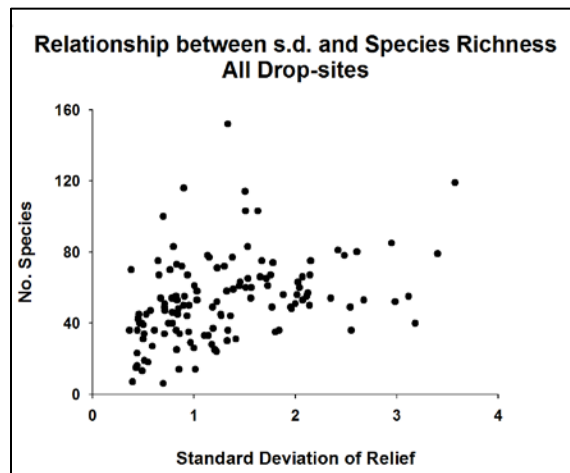


Figure 28. Graphs: relationship of SDR on a bank & species richness and of species richness as function of SDR.

(A) Graph of the relationship between the SDR on a bank and species richness of the mesophotic sessile epibenthic community. (B) Similar graph of species richness as a function of SDR, but at the drop-site level of spatial resolution.

About (A): Based on preliminary data drawn from Horseshoe Bank, encompassing 3–4 drop-sites or 35 transects. Highly significant correlation ($p < 0.001$, $r = 0.742$, Pearson's product-moment correlation analysis) and highly significant asymptotic curve describing relationship ($y = -11.51 + 54.38[1 - e^{-0.50X}]$, $p < 0.001$).

About (B): Data drawn from all drop-sites within all banks (n = 129). Highly significant correlation ($p < 0.001$, $r = 0.381$).

When species richness was considered as a function of the SDR at the bank level of resolution, once again, a highly significantly positive relationship emerged (Fig. 29; $r = 0.61$, $p < 0.05$; Model II regression, $y = 62.11 + 54.06X$, $p < 0.05$). This relationship was linear.

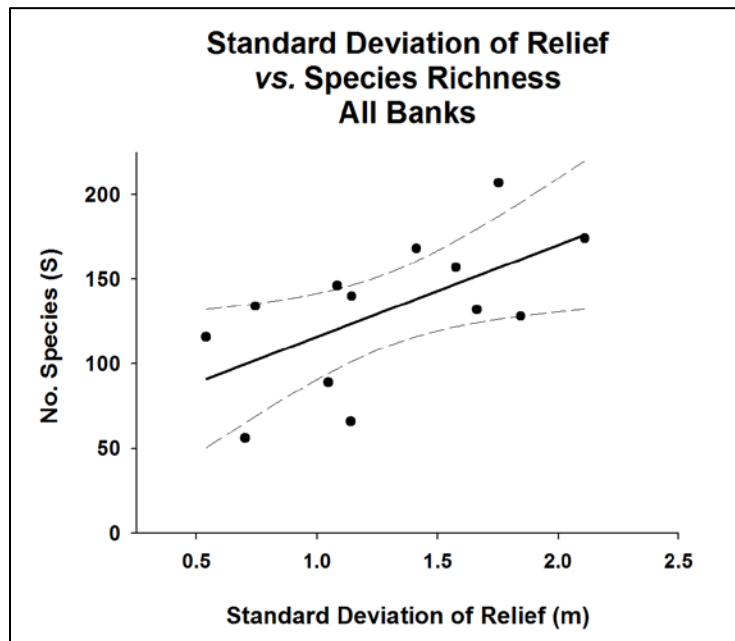


Figure 29. Graph: relationship between SDR and species richness of the mesophotic sessile epibenthic community in the Gulf Mexico, at the bank level of spatial resolution. All 13 study banks shown. Significant correlation between the two variables ($r = 0.611$, $p < 0.05$, Pearson's product-moment correlation analysis). Also, significant positive Model II linear regression analysis ($p < 0.05$, $y = 62.11 + 54.06X$). 95% confidence bands also shown for regression line.

It should be noted that there no significant relationship could be discerned between species richness and benthic relief at the level of transect or drop-site within banks ($p > 0.05$, Pearson's Product-Moment Correlation Analysis). There was, however, as has been shown above, a clear positive relationship between these two variables at the inter-bank level.

When species richness was plotted against latitude, no significant pattern emerged (Fig. 30a; $r = -0.29$, $p > 0.05$). When species richness on the banks was plotted against longitude, there was also no significant relationship (Fig. 30b; $r = -0.04$, $p > 0.05$) and no apparent E-W trend.

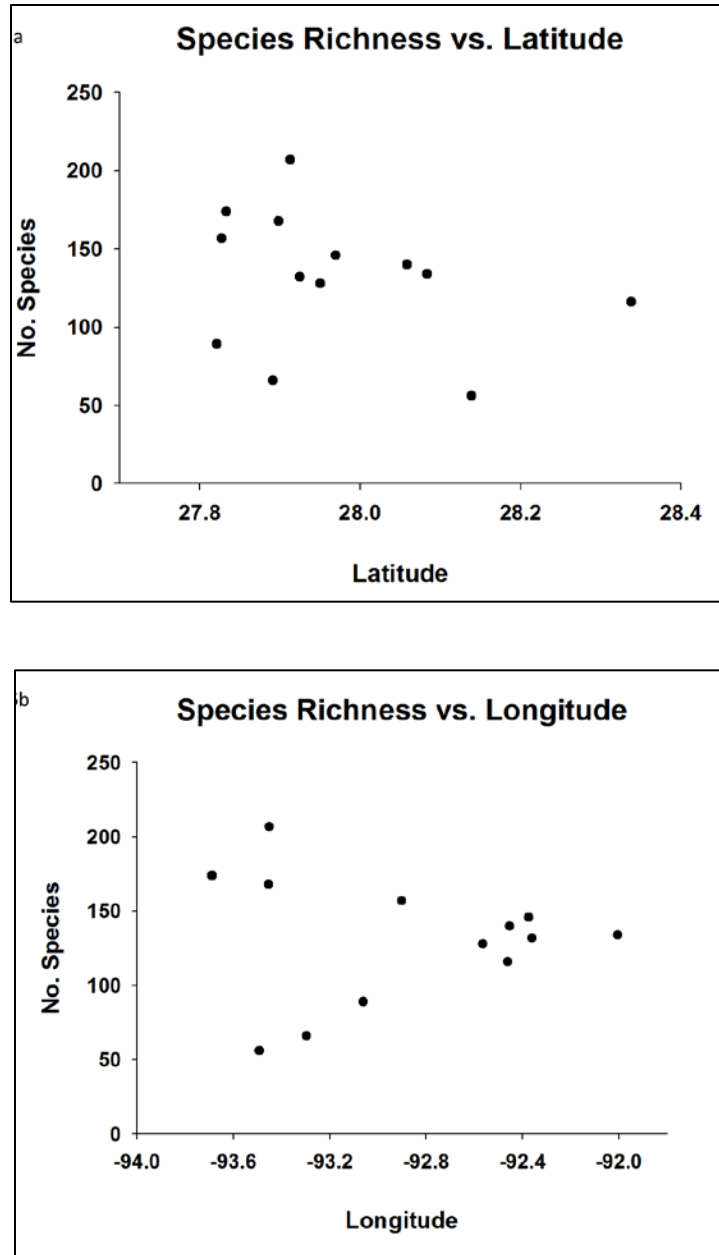


Figure 30. Graphs: species richness of the mesophotic sessile epibenthic community as a function of latitude and of longitude over the study area

(A) Species richness of the mesophotic sessile epibenthic community as a function of latitude over the study area (215 km, E-W). No significant correlation between the two variables ($p > 0.05$). (B) Species richness of the same community as a function of longitude over the study area. Also no significant correlation between the two variables ($p > 0.05$).

3.3.3 Geographic Patterns: Three-way Analyses

When species richness, latitude, and longitude were plotted in 3-D, an interesting pattern emerged. When we consider species richness as a function of geographic distribution over the

entire study region, we find a broad peak in the east, south of Grand Chenier, Louisiana, and another peak in the southwest, south of Port Arthur, Texas, separated by a deep trough (Fig. 31a). When considering the mean relief of the bottom throughout the entire study region, a very similar pattern of peaks and a trough became evident (Fig. 31b). When we considered the SDR on the banks, a pattern almost identical to that of mean relief emerged (Fig. 31c).

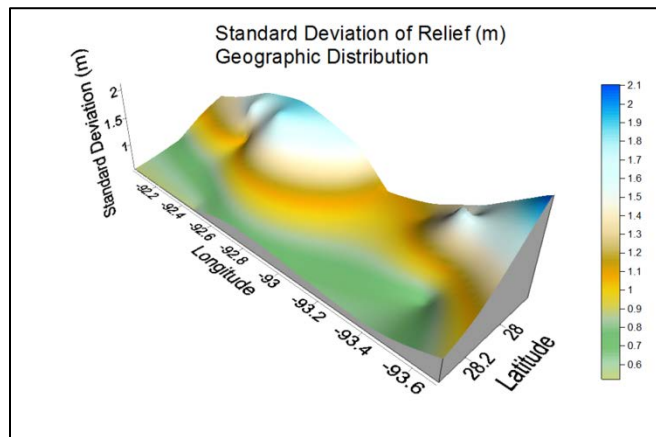
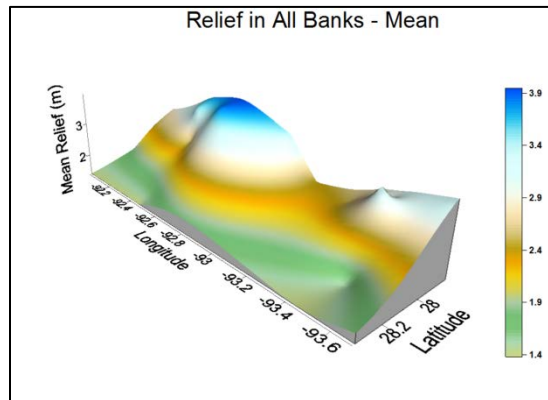
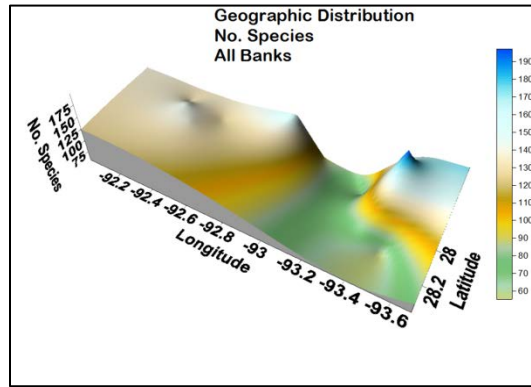


Figure 31. Graphs: degree of species richness of the mesophotic sessile epibenthic community, mean relief of the study banks, & SDR of the study banks.

(A) Degree of species richness of the mesophotic sessile epibenthic community on the study banks as a function of geographic position over the study area (215 km) in the Gulf. Note peaks in the eastern sector and the southwestern sector, and the trough between them. (B) Mean relief of the study banks as a function of geographic position on the continental shelf over the study region (215 km). Note similarities between the pattern of relief in (B) and that of species richness in (A). (C) SDR of the study banks as a function of geographic position on the continental shelf over the study region. Note similarities between this pattern of relief and that of mean relief (B) and species richness (A).

4. DISCUSSION

4.1 Comparative Relief on Banks, Including Geographic Patterns

4.1.1 *Relief on the Banks and Their Predictability*

The outer-shelf and shelf-edge banks in the northern Gulf vary greatly in the degree of relief characterizing them. There is a graded distribution of relief among these banks. Relief is fairly variable and not biased towards low or high values per bank in this study area.

Note that a description of physical relief on these banks and their variance will be provided here in detail. These data will then be correlated with species richness below to demonstrate any statistically significant relationship between the two. Data will be presented below on relief and associated species richness characteristics for each of the banks. If the correlations are significant, this, in turn, may provide some degree of predictability of species richness on the individual banks based upon their relief characteristics. Here, however, we will concentrate on physical relief characteristics only.

The above patterns were generally similar between mean relief and the SD index. In fact, throughout the study, the SD generally tracked patterns in mean relief, making the two measures equally good indices for this attribute. In a number of cases, the SD emerged as the more sensitive indicator of relief of the two.

At the high end of relief, Sidner Bank had drop-sites with the highest values – with averages of 6.4 m in mean height, sometimes reaching 9.0 m. This is substantial variation. Relief at other drop-sites on the reef, however, ranged down to a mean of 2.2 m, with individual transects containing minor height variations from the bottom as low as 0.5 m. Data derived from the SD echoed this pattern. SD's for individual drop-sites, however, were generally lower than the means in value and their 95% confidence limits were more compressed. Sidner Bank is not a salt dome. It is a tilted fault block composed of sedimentary rock which has been uplifted on its east side, and is bounded by several faults. Rezak et al. (1985) report that its relief is due to erosion, faulting, and some carbonate growth, all of which have been subjected to uplift and tilting through various sea level rises and falls. Gas vents have also been observed there. All of these factors could have contributed to the degree of, and variation in, relief observed here.

The relief data collected here indicate that, in most cases, it is impossible to predict degree of relief for an entire bank on the basis of limited surveys or a survey of one or a few drop-sites. A broader survey is required. The only exceptions here were one low-relief bank - Sonnier Bank - and one relatively high relief bank – McGrail (see below).

On 29-Fathom Bank, all drop sites exhibited extraordinarily low relief, irrespective of the index used to estimate such. The consistency between drop-sites was much higher than on, for example, Sidner Bank. Variability between transects can still be substantial, though, as was the case with Transects #3 and #6. Despite the overall predictability of relief on the basis of its mean, it is still recommended that a number of transects and drop-sites be used to characterize such a bank.

On Bright Bank, a bank of intermediate relief, the range of relief values along with their 95% confidence limits was broad (using either measure). The range of means and SD for individual transects was also highly variable. Thus, a number of transects and drop-sites must be used to characterize a drop-site on most of these banks, for no one transect of only several minutes duration would be sufficient to characterize relief of a drop-site. Bright Bank shows us that a bank with intermediate relief may possess as many low relief sites as high ones and will require a replicated survey in order to obtain an understanding of the bank's overall relief and associated species richness. Table 14 and Figure 23 demonstrate the variation in both of these characters.

The other 11 banks varied in relief between values reported for 29-Fathom and Sidner Banks. Mean of a transect or of a drop-site or SD worked equally well as indicators on these banks. At the low relief end, any differences in Sonnier Bank's mean relief or SD were almost imperceptible, and any one drop-site would be almost as descriptive of the bank as another. Sonnier is considered to be a mid-shelf bank associated with a salt diapir with outcrops of Tertiary limestone, sandstone, etc. It is characterized by several peaks in an arc pattern rising from ~60 m, most likely created by the collapse of the salt diapir. This has most likely contributed to the variance in the relief patterns observed.

Alderdice Bank was another lower relief bank, and this concurs with Rezak et al.'s (1985) observations of small-scale ridges and peaks. It exhibited reasonable differentiation between drop-sites. It has sides which increase with depth and occurs on an uplifted salt-dome. It is characterized by an annular fault, encircling the bank, as well as radial faults with recent displacement (Rezak et al., 1985). Sedimentation has been active there, although such has been disrupted by dynamic upward diapirism. All of these things may have affected relief on this bank.

The trend of increasing variability in relief on these reefs became more exaggerated with Rezak and Bouma Banks through to 28-Fathom, Horseshoe, Geyer, Elvers, McGrail, Parker, and Rankin Banks, respectively. With respect to Geyer Bank, it is characterized by a host of unusual depths due to its position in the northeastern part of an arced complex of salt diapirs (Rezak et al., 1985). It is fault bounded caused by upward thrusts of the salt diapir. It has outcrops of nearly vertical beds and steeply dipping sequences, most likely caused by collapse of the bank crest due to salt dissolution. These movements are suspected to be recent because of observations of bare rock outcrops. Gas seeps have been observed there. The steep slopes are most likely fault scarps. All of these characteristics could have influenced the degree of relief on this bank and ones like it. Rezak Bank has similar characteristics to Sidner Bank (see above), as they have been considered part of the same geological structure (Rezak et al., 1985).

Only in rare instances could relief of a bank be predicted from one or two transects or one or two drop-sites. In almost all cases, a number of transects within numerous drop-sites would have to be sampled in order to gain an understanding of the range of relief of the bank and its degree of variability (see Table 16).

Table 16. Details of each bank in the Gulf studied here.

Includes latitude and longitude of location, value of mean relief of each bank, SDR for each bank, species richness or no. species of the mesophotic sessile epibenthic community on each reef, no. of drop-sites sampled on each bank, and no. transects sampled per bank. Banks shown in alphabetical order.

Bank	Latitude	Longitude	Mean Relief (m)	Standard Deviation of Relief (m)	No. Species	No. Dropsites	No. Transects
28 Fathom	27.8978	-93.4525	2.93432121	1.41153141	168	11	53
29 Fathom	28.1388	-93.491	1.498676689	0.700873859	56	10	50
Alderdice	28.0839	-92.0035	1.816045809	0.742785327	134	10	50
Bouma	28.0582	-92.4539	2.486438571	1.14346406	140	10	45
Bright	27.8916	-93.2955	2.517272238	1.139496982	66	10	50
Elvers	27.8275	-92.9001	3.430118953	1.575584509	157	10	46
Geyer	27.8214	-93.0607	2.393549193	1.045168348	89	10	50
Horseshoe	27.8332	-93.6875	3.351127373	2.109871705	174	10	70
McGrail	27.95	-92.565	3.845958943	1.843363648	128	10	50
Rankin	27.9132	-93.4496	3.415833835	1.753083556	207	10	51
Rezak	27.9693	-92.3738	2.568782584	1.081606646	146	8	40
Sidner	27.925	-92.36	3.497718683	1.661761832	132	10	50
Sonnier	28.3378	-92.4616	1.378548166	0.539983972	116	10	50

This variability in relief on banks implies that there may well be concomitant variation in benthic biodiversity. If this is the case, and if the correlations were significant, this could provide valuable information, to the oil and gas industry regarding where or where not to drill based upon geomorphological data alone. Such would provide both substantial time- and cost-savings. These relationships will be discussed below at several scales of spatial resolution.

4.1.2 Geographic Patterns in Relief and Potential Causal Factors

Some of the most interesting information to emerge from this study is the geographic pattern in relief of the banks surveyed. The latitudinal trend of decreasing relief (mean or SD) in the study region as one moves northward from the edge of the continental shelf onto the shelf is clearly evident. This is consistent with observations made by Rezak et al. (1985). The trends in longitudinal patterns of relief are even more intriguing. As one moves from west to east, from south of Port Arthur, Texas to south of Lafayette, Louisiana – over 215 km, low relief areas may be seen off Calcasieu Lake, Louisiana and Lafayette. It is important to recognize that these are not trends in depth but in relief on the banks.

What has caused geographic variation in the relief of these banks? A number of processes have been identified above which could have influenced degree of relief on a bank or reef in this study area. They include faulting, dissolution of salt in a diapir and subsequent collapse of a portion of the bank, erosion, calcium carbonate accretion, sediment accumulation, etc. Any one or all of these processes could affect the observed patterns of relief on a given reef, or indeed the pattern observed over the region.

In addition to these processes, Roberts et al. (2010) and Roberts (1992) have reported that these banks most likely originated in deep water by the precipitation of authigenic carbonates at hydrocarbon seep sites (also see Roberts and Whelan, 1975; Roberts et al., 1987, 1988). Nearly all of the banks mentioned in this study have hydrocarbon seeps associated with them – mostly gas and some oil. It is known that microbes are involved in degrading hydrocarbons and subsequently producing calcium carbonate. Such processes have been observed not only here but in other parts of the world (Wada and Okada, 1982; Hovland et al., 1987). Other studies have shown that, once the banks extended into shallower water, particularly during the Pleistocene, they became coral reefs, which are now relic or drowned reefs (see Ritchie et al., 2008; Blanchon et al., 2009; Locker et al., 2010). These reefs generally fall in the 60-120 m depth range (Rezak et al., 1982). It is possible that another factor could have contributed to differential growth rates of these banks and degree of relief; this might have been variation in rates of carbonate accretion.

Also, this region experienced a sea level change of ≥ 100 m below present sea level 14,000-20,000 years ago during the Pleistocene (Ahr, 1973). It is possible that, during a period of low seawater stand, as noted above, these areas were subjected to the flow of ancient rivers over the exposed land of which is today the continental shelf (Mange and Otvos, 2005) and were subjected to erosion (e.g., Thunell, 1976). The shore at that time would have been at what is now the continental shelf edge (Rezak et al., 1985). The areas in question coincide with the ancient deltas of the Mississippi River and “Delta C”, as described by Suter and Berryhill (1985).

In addition, it is possible that there may have been differential sedimentation by rivers as sea level dropped toward the late Pleistocene glacial maximum (Kennett and Huddleston, 1972). The cline in N-S relief may also be related to the duration of historical flooding in this region (Galloway, 1989). Banks at the shelf edge were submerged the longest and therefore could have developed relief-building communities over the longest period of time. Coring these banks would most likely help to define the reef-building processes related to sea level variation.

The E-W variations at the shelf edge may be related to Loop Current eddies and the introduction and maintenance of warm seawater temperatures (Oey et al., 2005). The highest relief areas may represent regions where the true carbonaceous reefs existed and flourished. This would have required sustained bathing in warm water which could have been provided by Loop Current eddies. These eddies are warm-water physical oceanographic features which move to the western Gulf, where they stall and dissipate, becoming trapped between the western and northern parts of the continental shelf edge. This would have provided a habitat where warm-water temperatures were maintained above the threshold necessary for sustaining reef-building corals (16°C).

Bottom areas with varying degrees of relief such as these banks occur all the way to the basin floor, to the south of the Sigsbee Escarpment and beyond (Niedorodo et al., 2003). How the banks examined here at the shelf edge vary from their deeper-water counterparts remains to be illuminated.

4.2 Patterns of Mesophotic Benthic Community Structure

4.2.1 Bank Groups

In the dendrogram, PATN[®] identified the majority of banks (10 out of 13), or at least the flanks of these banks which we surveyed, as being indistinguishable from each other with respect to species composition and abundances. At the other end of the spectrum were 29 Fathom and Sonnier Banks, which were characterized by a different set of species. Geyer Bank, on the other hand, fell between these two sets of banks as a sole representative of its Bank Group (#2). In that case, Geyer was characterized by its low representation of fauna and flora and a unique set of abundant species. Thus, we have three major groups of banks – one large one, driven primarily by Species Group 4; another single bank, driven by low biodiversity and a mild forcing by Species Group 4; and another driven by Species Group 2 and a low level of Species Group 4.

The grouping of banks was described in even greater detail by values produced within the Dissimilarity Matrix, produced through all pairwise comparisons. There, the first group of banks, Sonnier and 29 Fathom, were characterized by high dissimilarity values. This was mimicked by Geyer Bank in the second Bank Group. The remaining 10 banks all had low values over the same pairwise comparisons.

4.2.2 Geographic Pattern

Additional insight regarding the Bank Groupings indicated within the dendrogram emerged when the banks and their group identities were placed into a geographic context. It became obvious that most of the banks – the 10 which fell into Bank Group #3 – were all located at or near the edge of the continental shelf. This region is characterized by warm, relatively clear seawater derived ultimately (Schmitz et al., 2005) from the Caribbean Current. Indeed, it is one of the reasons why the FGB (near Horseshoe Bank) are 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 did not develop as a true coral reef with a carbonaceous cap during the Holocene (Zingula, 2008, 2015). This is primarily because of its local environmental conditions, particularly temperature, which are sub-optimal for development. The two banks in Bank Group #1 – 29 Fathom and Sonnier – both occur further 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, due to inshore cooling during the winter (Pulley, 1963; NOAA Flower Garden Banks National Marine Sanctuary, 2014b). The benthic fauna and flora is different there than at the shelf edge.

Geyer Bank is the stand-alone bank which falls geographically in the middle of the remaining 10 banks at the shelf edge. It is positioned at the shelf edge, and, despite this, has 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 than on the other banks. The low biodiversity of fauna and flora there

caused PATN[®] to separate it out from the other banks. At this time, the historical or current, biological and/or physical factors or events causing this variation from other banks is not known.

4.2.3 Species Groupings and Box-and-Whiskers Analyses

The two-way table describing species, their abundances, and their influence in defining Species Groups, provides information on which species or taxa were critical in defining those 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 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 and #3 were consistently characterized by very low abundances of all species, although the species composition was different in each group. Species Group #2 was somewhat intermediate, with several dominant species but had relatively low abundances in all other species. The species composition there varied from other Species Groups. The box and whisker analyses further illuminated these trends.

The summary of the five most dominant species on each bank (Table 10), in comparison to the two-way table (Table 8) produced by PATN[®], revealed some interesting patterns in the data. Firstly, the dominant species on each bank may have helped to define the Bank Groupings produced, but ultimately it was a series of contributing factors that did so. These would have included the dominant species, the entire array of species present, overlap of species between sites, and the species richness on each bank.

The best developed of the banks appear to be those at the edge of the continental shelf. This has also been shown for the coral communities living on oil and gas production platforms in the same region (Sammarco et al., 2004, 2012). Two of the banks in Bank Group #1 (29 Fathom and Sonnier Banks) were quite different in their community composition from the 10 banks in Bank Group #3. These banks occurred further north on the continental shelf, closer to shore. This more northerly region is not immersed in outer-shelf edge or Gulf 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 remain unknown at this time.

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 region are healthy diverse communities, qualifying as confirmed sensitive benthic communities. They may warrant additional protection. These surveys, of course, only considered hard-bottom on features with any relief. It is recommended that surveys also be performed on soft-bottom in this region on these or similar reefs. This is because they may also harbor abundant populations of benthic organisms meriting protection.

4.2.4 Percent Cover of Live Sessile Epibenthic Fauna and Flora

Percent-cover of live sessile epibenthic fauna and flora on the study banks was relatively low, never reaching an average higher than 26.5% on any individual bank and 36.0% on any individual drop-site (see Table 13). Hard-substratum which is sediment-free is relatively rare in these deeper-water environments, where current velocities are low and sedimentation rates are high. Thus, clear hard substratum, in fact, becomes a limiting factor for larval recruitment and community development for these organisms. Nonetheless, the species richness levels, overall, were relatively high (see below) and make up for the overall low percent-cover.

4.2.5 Relationship between Benthic Relief and Percent-Cover of Sessile Epibenthic Fauna and Flora

The positive relationship between mean benthic relief and percent-cover of sessile epibenthic fauna and flora supports the above conclusions. Increased relief of the bottom will most likely result in a decrease in cover of sediment-covered hard substratum due to sloughing. This releases more substrate for colonization and growth of the epibiota. The relationship is robust as it was evident at both the individual bank and individual bank levels of resolution.

4.2.6 Habitat Characterization Using Species Richness

The techniques used here – 3-D graphing – facilitated characterization of habitats for sessile epibenthic community development on the banks, using species richness as a metric. By using this type of graphic, it was possible to gain an understanding of the distribution of species richness within a bank, and where peaks in species diversity as well as low diversity areas occurred. In our case, the distribution of species richness varied widely within each bank. Clearly, some areas were better for benthic community development than others on each bank.

Comparing banks with respect to distribution of species richness provided revealing information. The patterns resulting from these comparisons demonstrated that one can find some very similar orientations, such as in 29 Fathom, 28 Fathom, Bright, McGrail, and Rankin Banks, whose peaks were in the northwest, while another set had a completely different orientation to the southeast (Alderdice, Bouma, Geyer, and Sonnier Banks). The miscellaneous orientation of the other four banks which varied from north to south in their peaks (Elders, Sidner, Horseshoe, and Rezak Banks), demonstrated that this character is highly variable. It is possible that these inter-bank patterns of species richness peaks are influenced by local meso-scale currents around each bank. It is known that laminar far-field currents, when impinging upon an obstacle such as a bank, can cause eddies in the lee of the obstacle (Black and Gay, 1987a,b; Andrews et al., 1989; Black et al., 1990; Gay and Andrews, 1994). It is also known that those eddies can entrain larvae, concentrating them and causing high levels of settlement in that region (Hamner and Hauri, 1981; Black, 1988; Sammarco and Andrews, 1988, 1989; Wolanski et al., 1989; Black and Moran, 1991). The meso-scale circulation around these banks, however, is not well studied, but such studies may assist in understanding the observed phenomena.

The lack of an overall geographic pattern in the distribution of species richness over the study region suggests that local factors may be influencing these within- and between-bank patterns more than the overall long-shelf currents at the edge of the continental shelf.

4.3 Comparative Relief on Banks, including Geographic Patterns

There are two major findings here that will be discussed. The first is the relationship between relief on offshore banks and species richness there, and its implications. The second is geographic patterns with respect to these two variables, and their implications.

4.3.1 Relationship between Relief on Offshore Banks and Species Richness

With respect to the relationship between relief and species richness, preliminary data analyses indicated that a positive relationship between mean relief and species richness. This relationship was asymptotic, rising most rapidly at lower relief levels of 0 to ~4-5 m relief and then tapering off. This implies that once a certain degree of mean relief is reached, the addition of species richness was relatively small with increasing relief. The analysis of similar mean relief and species richness data, drawn from all drop-site data, further confirmed this relationship and indicated that it was more diffuse, with a higher degree of variance. Thus, when mean relief is used as a measure of relief on a bank, species richness at the bank level is a much more reliable metric and indicator of species diversity than at the drop-site level. This is most likely because much of the variance in the data has been averaged out when calculating the bank means. This relationship also implies that high relief features or PSBF areas merit protection from physical disturbance, as they are the most species-rich. This is not to say that areas of lower relief do not merit protection; only that those areas with higher relief should probably merit priority.

The fact that a clear positive linear relationship was revealed when species richness, considered at the bank level and for all banks, was plotted against mean relief on the banks implies that species richness can indeed be predicted from mean relief on these banks. In addition, it implies that this general relationship is applicable across a broad geographic region (215 km).

The fact that the relationship between the SDR and species richness was very similar to that of mean relief and species richness confirms reinforced the finding that that relationship is positive and asymptotic. The point of inflection in that curve occurred at approximately ~2-3 m relief. Species richness as a function of SDR at the drop-site level confirmed that these data were highly variable at this level of spatial resolution. This implies that this level of spatial resolution provides a less precise index.

When considered at the bank level, the data revealed a significantly positive and linear relationship between species richness and SDR, which indicates that this level of resolution would serve as a good indicator of species richness. In addition, the variance in species richness was lower and the slope of the curve higher. Thus, the SDR yields a clearer, stronger relationship with species richness than mean relief, and one which is less variable.

Using the full data set (compared to the preliminary data set discussed above), we could not detect any relationship between species richness and benthic relief at the transect or drop-site levels of spatial resolution. We could, however, detect such at the bank level of resolution. This indicates that the variance in both species richness and benthic relief was simply too high to permit detection at these first two levels of spatial resolution. That is, the “signal-to-noise” ratio was simply too low. When one considers the relationship at the bank level, however, where the data from 50 transects and 10 drop-sites within a single bank are combined, the positive relationship between species richness and relief becomes clear – even with a sample size of only

13 banks. This means that the relationship is robust – and reliable. It is, of course, not without variance, but the link between the two variables is clear. At this point, it is not known whether there is a relationship between species diversity, relief, and total bank area.

4.3.2 Co-varying Geographic Patterns in the Relationship between Relief and Species Richness

The search for geographic patterns in the species richness data at first yielded confusing results but then revealed an important relationship. Examining the relationship between species richness and latitude yielded no significant pattern, and this was mimicked when considering longitude. It was not until species richness was considered over the entire 215 km-long study area using a 3-D representation of the data that trends became apparent. Here, peaks in species richness became apparent on the western side of the study area and on the southeastern side. In addition, there was a clear trough between the two peaks, at -93.2°W longitude, extending latitudinally across the entire study area. It was not until this information was reviewed in concert with a similar 3-D depiction of mean relief on all banks over the study region in a geographic context that the relationship became clear. The peaks in mean relief were very similar to those in species richness, and remarkably so in the western third of the study area. The fact that this was mimicked when the SDR was used as a metric in the analysis underscored this result. It would appear that relief is having a major effect on the species richness of these banks at this broad spatial scale.

Thus, it appears that relief, particularly as measured by the SD, can act as a good indicator of species richness. This is particularly pertinent to offshore banks in the Gulf, although it may also apply to other banks and reefs. In addition, benthic relief can be an equally good indicator of species richness at the scale of km, tens of km, and hundreds of km, representing a particularly robust relationship that may be applied at a number of spatial scales. That is, the linear and non-linear models presented here reveal the types of relationships which exist on the flanks of offshore banks, and it may be possible to use relief data from bathymetric maps or even low-altitude remote sensing to draw conclusions about species richness of the benthos based on relief data.

5. CONCLUSIONS

5.1 Comparative Relief on Banks, Including Geographic Patterns

- . We performed fine-scale surveys of relief on the flanks of 14 banks in the Gulf to examine variation between them, geographic patterns, and possible processes influencing their formation: 28 Fathom, 29 Fathom, Alderdice, Bouma, Bright, Elvers, Geyer, Horseshoe, Parker, Rankin, Rezak, Sidner, and Sonnier Banks.
- . Sidner and McGrail Banks had the highest relief, 29-fathom and Sonnier the lowest. Sidner Bank had relief averaging up to 11m in height, while 29 Fathom Bank exhibited the lowest relief (range 1.2-2.2m).
- . Bright Bank exhibited intermediate and variable relief at both the transect and drop-site levels.
- . Relief is not predictable on many of these banks due to high variability between drop-sites.
- . Regarding geographic patterns, relief decreased significantly as one moved northward. Relief exhibited a significant sinusoidal pattern from west to east.

5.2 Patterns of Mesophotic Benthic Community Structure

- . We surveyed sessile epibenthic communities on the flanks of the above 13 banks to determine species richness, species composition, similarities between benthic communities, and geographic patterns in community structure.
- . The banks were as above, except for Parker Bank, totaling 13 banks.
- . Data were analyzed via PATN[®], which revealed three main Bank Groups: #1 containing 29 Fathom and Sonnier Banks; #2, Geyer Bank; and #3, the remainder.
- . 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 was the largest (containing *Elatopathes abientina*, *Nicella* sp., *Peysonellia* sp.), primarily defining Bank Group #3. Species Groups #2 (e.g., *Antipathes* sp.) and #3 (low species abundances) were associated with Bank Group #3. Species Group #4 (low species richness) was a major contributor to Bank Group #2 (Geyer Bank). Species Group #2 was the primary constituent of Bank Group #1, also characterized by low species richness.
- . Most species had a comparative abundance of $\leq 20\%$.
- . The high species richness and affinities exhibited by Bank Group #3 are probably due to continual exposure to warm, low turbidity Caribbean water at the shelf edge.
- . Based upon data derived from the literature, banks inside the shelf probably vary from the others due to exposure to cooler winter temperatures and higher turbidity due to wind-forced inshore water. (No environmental data were collected during this study.)
- . Reasons for the unique community structure on Geyer Bank are unknown.
- . Percent-cover of live sessile epibenthic fauna and flora is relatively low on the banks, never exceeding an average of 26.5% on any one bank. It varies highly significantly between banks. Its variance is also low.

- . Percent-cover of live sessile epibenthic fauna and flora is highly significantly correlated with benthic relief, both at the bank and drop-site levels of resolution. This is most likely due to sloughing of sediment with increased relief.
- . Of the species or taxa encountered in this study, 42 were found to be protected under CITES. Additional rare or endemic species were also found.

5.3 Comparison of Relief and Species Richness on Banks, Including Geographic Patterns; Relationship between Physical and Biological Factors

- . We gathered information on bottom relief at a small scale (~210,000 points) and species richness of the sessile epibenthic community using a remotely operated vehicle.
- . We surveyed the hard bottom on flanks of the above 13 banks in the north-central Gulf, generally below 27 m depth, on the continental shelf and at the shelf edge extensively.
- . Initial analyses indicated an asymptotic relationship between mean relief and species richness at the transect level.
- . Secondary detailed analyses at the drop-site level revealed a similar relationship, although variance was higher.
- . At the bank level, the relationship between mean relief and species richness was positively linear.
- . Analyses using the SDR yielded similar results, except that the positive linear relationship became stronger.
- . No significant trends were apparent when benthic species richness was considered in a two-way analysis with respect to latitude and longitude, respectively, over the geographic range of the study area (215 km).
- . When species richness was plotted in 3-D, however, peaks in species richness emerged in the southeastern study area and the western region, with a trough between them. This pattern coincided well with bottom relief.
- . Species richness is positively correlated with bottom relief on banks in the northern Gulf. It may also be predicted at a number of spatial scales, up to hundreds of km, based on bottom relief.

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island communities.

The Bureau of Ocean Energy Management Mission

The Bureau of Ocean Energy Management (BOEM) works to manage the exploration and development of the nation's offshore resources in a way that appropriately balances economic development, energy independence, and environmental protection through oil and gas leases, renewable energy development and environmental reviews and studies.