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Evaluating the Efficacy of Using Geomorphology as a Surrogate to Benthic Habitat on the Miami Terrace

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Thesis of
Kim D. Smith

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

May 2018

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Thesis Committee

Major Professor: Dr. Brian Walker, PhD

Committee Member: Dr. Charles Messing, PhD

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HALMOS COLLEGE OF NATURAL SCIENCE AND OCEANOGRAPHY

**EVALUATING THE EFFICACY OF USING GEOMORPHOLOGY AS A
SURROGATE TO BENTHIC HABITAT ON THE MIAMI TERRACE**

By

Kimberly D Smith

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
In partial fulfillment of the requirements for
The degree of Master of Science with a specialty in:

Marine Biology
Nova Southeastern University

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Table of Contents

List of Figures	2
List of Tables	2
Acknowledgments	3
Abstract	4
1. Introduction	6-13
2. Methodology	13-19
3. Results	19-33
4. Discussion	33-40
Literature Cited	41-44

List of Figures

Figure 1. Map of the Miami Terrace.....12

Figure 2. Map of the area of high resolution bathymetry from the Miami Terrace.....13

Figure 3. Map displaying the spatial arrangement of the Miami Terrace transects.....16

Figure 4. Flow chart illustrating procedure for statistical analysis.....18

Figure 5. A nMDS plot illustrating similarity of transects by geomorphologic region and slope.21

Figure 6. A nMDS plot illustrating transect species density similarity with respect to three depth bins representing differing depth ranges.....22

Figure 7. A nMDS plot illustrating the variance of transect species density with respect to majority cover23

Figure 8. Pie charts for percent cover proportions of each transect.....24

Figure 9. A nMDS plot illustrating the influence of the species contributing at least 75% to variance in transect similarity26

List of Tables

Table 1. Community and Environmental Details by Transect.....25

Table 2. Variance of Average Organism Density Across Geomorphologic Classes for Most Impactful Species.....26

Table 3. Results of One-Way ANOVA or Kruskal-Wallis Test by Region29

Table 4. Results of Tukey's HSD Test by Region29

Table 5. Results of One-Way ANOVA or Kruskal-Wallis Test by Slope30

Table 6. Results of Tukey's HSD Test by Slope.....31

Table 7. Results of Correlation between Percent Cover Soft bottom and Organism Density33

Table 8. Results of Correlation between Percent Cover Hardbottom and Organism Density.....33

Table 9. Results of Correlation between Depth and Organism Density33

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Abstract

The deep-sea is a vast and relatively sparsely characterized domain. As little as 0.01% of deep-sea benthic habitats have been characterized in detail. Characterizing the distribution of organisms and environmental components of the deep-sea is pivotal to the creation and implementation of successful resource management. Benthic habitat maps are a good method to inventory and characterize deep-sea habitats. Recent advances in technology, such as multibeam sonar and remotely operated vehicles (ROVs), have allowed for greater understanding of these ecosystems. As it is difficult and expensive to collect data deep-sea benthic community composition, environmental surrogates of biological data would be economically beneficial. Ideally, a surrogate is an easily-measured abiotic indicator that greatly influences benthic community composition. The quality of a surrogate can be extrapolated to represent the quality of benthic habitat.

The Miami Terrace is a deep-sea ecosystem that has begun to be explored and characterized. Previous studies noted that community compositions vary with broad-scale geomorphology on the Miami Terrace. This study addresses a swath of data collected from the Miami Terrace to determine if geomorphology in high resolution bathymetry could serve as a viable surrogate to biological data for the initial characterization of benthic habitats on the Miami Terrace. Data from cable impact assessment surveys for the South Florida Ocean Measurement Facility (SFOMF) and the Department of Energy were utilized in this study. Images from these surveys were analyzed to generate and detail twelve transects across a section of the Miami Terrace. This cross section of the terrace had previously been sectioned into distinct geomorphologic zones (Messing et al., 2012). The geomorphologic zones assessed in this study were High Slope Inner Terrace (HSIT), Low Slope Inner Terrace (LSIT), High Slope Outer Terrace Platform (HSOTP), Low Slope Outer Terrace Platform (LSOTP), High Slope Outer Terrace Ridge (HSOTR), and Low Slope Outer Terrace Ridge (LSOTR). Images from these transects were analyzed to generate percent cover and community data. This data includes overall organism density, species richness, and an inventory of all organisms greater than 4 cm identified to the lowest taxonomic level possible. This data was taken in concert with previously collected environmental data (e.g. depth, slope, and geomorphology) and subjected to multivariate statistical analysis.

Patterns in organism density across the transects align with the progression of the transects by slope and geomorphologic region. Depth was seen to increase from Inner Terrace to Outer Terrace Platform. The Outer Terrace Ridge exhibited an increase in the percent cover of hardbottom habitat; which is preferential for many organisms. This corresponded to a shift in the organism density of multiple Cnidarians and Poriferans. In particular, the density of stylasterids and several sponges increased towards the Outer Terrace Ridge. One High Slope Inner Terrace transect juts into the Outer Terrace Platform, and it was more similar to Outer Terrace Platform transects than those of the Inner Terrace. This suggests that area of Inner Terrace jutting into the Outer Terrace Platform may need to be reassigned as Outer Terrace Platform.

Analysis of variance by region and slope yielded that the density of multiple species varies with geomorphology across the study area, and high slope areas had significantly higher species richness than areas of low slope. These results support that geomorphology could serve as a surrogate for the Miami Terrace; however, it is likely a combination of geomorphology and another environmental factor (e.g., percent cover substrate or depth) would better serve to predict distribution of species on the Miami Terrace. The results of this study support that

geomorphologic region, slope, depth, and percent cover of substrate can be used to determine different deep-sea habitats on the Miami Terrace. The influence of geomorphology on organism densities was varied, and thus its predictive capacity and efficacy as a surrogate remains limited. Nevertheless, the necessity for ecological baselines to guide management decisions is greater than the uncertainty associated with the use of geomorphology as a surrogate on the Miami Terrace.

Key words: Deep-sea, habitat characterization, multivariate analysis

Introduction

The world ocean is a dynamic and powerful influence on the environmental conditions of the earth. Marine ecosystems are the prevailing habitat on the planet, and the vast majority of marine ecosystems exist beneath 200 meters. The land and water beneath this depth are known as the deep-sea. The deep-sea makes up more than 50% of the available habitat on the planet (Davies et al., 2007), and thus is considered the largest biome on Earth (Merrett & Haedrich, 1997; Webb, Berghe, & O'Dor, 2010). Despite being so expansive, there are large gaps in knowledge about the community composition of deep-sea habitats. These knowledge gaps can be attributed to the difficulties inherent in surveying an environment so distant from and inhospitable to man (Snelgrove, 1999). This knowledge disparity poses problems for policy makers and researchers alike who seek to understand how to best conserve and manage deep-sea environments.

A growing interest in deep-sea habitats has led to deep-sea exploration on a global scale; however, many of the deep-sea coral reefs recently discovered already contain significant damage from anthropogenic impacts (Frank et al., 2005). Deep-sea corals and hardbottom habitat provide habitat for economically important fish, and are highly susceptible to the damage caused by human activity such as fishing (Merrett & Haedrich, 1997; Andrews et al., 2002; Reed, Koenig, & Shepard, 2007; Brown et al., 2011). Deep-sea corals are slow-growing species that, in the case of *Leiopathes* sp., can be over four thousand years old (Roark et al., 2009). Damage caused to coral reefs in the deep can take tens or even hundreds of years to reverse due to this slow growth rate (Reed, 1981; Andrews et al., 2002; Rengstorf, Yesson, Brown, & Grehan, 2013). In addition to the damage caused to corals by anthropogenic influence, a number of deep-sea fish stocks are considered unsustainable or have already collapsed (Andrews et al., 2002). As

very few of these important deep-sea hardbottom habitats are presently characterized, it is critical to monitor and characterize these habitats to understand anthropogenic impacts on these environments, and to establish a baseline of deep-sea resources for management and conservation (Brown et al., 2011; Kostylev, 2012; NOAA, 2015).

Seafloor characterization is an essential step for understanding deep-sea benthic marine ecosystems, their extent, and their constituents (Flanagan & Cerrato, 2015; Shumchenia et al., 2015; Vasquez et al., 2015). Benthic habitat mapping is a means of characterizing the deep-sea seafloor (Harris & Baker, 2011). Benthic habitat maps are often used to visually represent the spatial arrangement of seafloor habitats, and they additionally may be used to quantify habitat and fauna (Harris & Baker, 2011; Walker, 2012). Despite the utility of benthic habitat maps, it is estimated only 5-15% of the seafloor has been mapped (Wright and Heyman, 2008; NOAA, 2015). The expanse of deep-sea habitats yet to be explored suggests that there may be far more species present and undiscovered in the deep than in familiar shallow waters. Indeed, it is known that more coral species are present in the deep-sea than in tropical coral reefs (Roberts et al., 2009). Recent technological advances have enhanced the potential for effectively characterizing and managing deep-sea resources (Rengstorf et al., 2013; Danovaro, Snelgrove, & Tyler, 2014). These include remote sensing technologies such as multibeam sonar and sidescan sonar systems (SSS) which can model and visualize seabed topography and hardness. Technologies such as remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), and submersibles provide means for in situ observations and sampling.

The most accurate benthic habitat mapping demands the integration of biological and environmental data from remote sensing and direct observation (Reed, Shepard, Koenig, Scanlon, & Gilmore, 2005; Rengstorf et al., 2013). For this reason, the development of

geographic information systems such as ArcGIS[®] has been pivotal to the characterization of deep-sea habitats. ArcGIS[®] allows for the visual integration of the environmental and biological characteristics of the seafloor in a way that is highly useful for spatial analyses (Greene et al., 2005). However, the direct observation of an ecosystem as distant and inhospitable to man as the deep-sea requires expensive operations and technology and an investment of time that often proves limiting or prohibitive (Wilson, et al. 2007; Menza, Kendall, & Hile, 2008; Bridge T, 2012). For this reason, deep-sea benthic habitat maps are generally derived from remote data that depict the topography of the seafloor over wide extents (NOAA, 2015; Vasquez et al., 2015).

A central design of most spatial ecological studies is to sample a population or an environment and then extrapolate those relationships to a broader area. The more efficient the data collection, the more efficient the extrapolations will be. Collecting data in the marine environment is inherently challenging and expensive, however it is exponentially so as depth increases. Therefore, deep-sea studies are often working with much less community sampling information than shallower studies. One method for building efficiency is to acquire and extrapolate environmental data that serves as a reasonable surrogate for difficult-to-acquire community data (Brown et al., 2011). Multibeam sonar has allowed for the imaging of the seafloor in unprecedented detail (Kostylev et al., 2001; Pickrill & Todd, 2003; Harris & Baker, 2011). In spite of the fact that accuracy of multibeam sonar is limited, and diminishes with increasing depth (Brown et al., 2011; Kostylev, 2012), the environmental characteristics that may be gleaned from multibeam sonar are highly valuable for benthic habitat mapping. These characteristics, including geomorphology and depth, can be used as predictors for species distribution. This can help to prioritize where expensive ground-truthing surveys would be most valuable (Pickrill & Todd, 2003; Wilson et al., 2007).

It is known that geomorphology contributes to the determination of the extent and composition of deep-sea communities. Geomorphology can be defined as “the scientific study of the formation, alteration, and configuration of seabed features and their relationship with the underlying geology” (Harris & Baker, 2011). To understand the geomorphology of an area it is necessary to address the interplay of factors including but not limited to depth, relief, geography, and substrate composition. This information is highly relevant to the distribution of organisms and the detailed characterization of habitats. It is important to consider geomorphology when addressing species distribution because many marine organisms relate to a particular geomorphology (Harris & Baker, 2011). This fact alone suggests that it is likely that a relationship exists between geomorphology and species distribution. Many studies across a multitude of benthic habitats have confirmed geomorphic features to be useful surrogates for community data (Harris & Baker, 2011).

Using geomorphology and depth as surrogates for community biogeography in deep-sea habitats facilitates the extrapolation of known community relationships across the seascape and provides economic benefit by limiting the area of seafloor that needs to be surveyed. My study evaluated the efficacy of using geomorphology as a surrogate for characterizing deep-sea habitats off the southeastern Florida coast in an area known as the Miami Terrace. It provides an assessment of the biological data on the northern Miami Terrace, and an understanding of how similar communities are between various geomorphologic classifications. My study contributes to a better understanding of regional deep-sea habitat biogeography throughout the Florida Straits.

The Miami Terrace:

The Miami Terrace is an area of drowned carbonate platform present in deep-water off the east coast of South Florida from Broward County to Northern Key Largo. It exists off the continental shelf at depths of 200-700 m (Reed, Weaver, & Pomponi, 2006). Portions of the terrace contain coral reef and hardbottom habitat that make it of particular interest for conservation (Andrews et al., 2002; Messing, Walker, & Reed, 2012). Efforts have been made to document community composition on the Miami Terrace, but a substantial gap in knowledge still exists concerning the benthic communities that inhabit the area.

The terrace itself is an irregular, elongated platform which parallels the east coast of Florida (Figure 1). It expands an area of approximately 740 km² with its widest point near its center offshore from Miami. From there, it tapers gradually as it extends north, and more severely as it continues south (Ballard & Uchupi, 1971; Mullins & Neumann, 1979; Messing et al., 2012). Mullins and Neumann sectioned the Miami Terrace into cross-shelf regions that spatially progress as the Upper Terrace, Outer Terrace Ridge, and Lower Terrace. The Upper Terrace lies at ~200-375 m depths and contains distinctive topography including the presence of sizeable outcrops and steep ridges. The northern Upper Terrace was divided further due to the presence of inner and outer platforms of differing depth, and the distinct biological communities noted therein (Messing et al., 2012). These regions were named Inner Terrace Platform and Outer Terrace Platform. Surveys were conducted in 2006 across a section of Inner Terrace Platform, Outer Terrace Platform, and Outer Terrace Ridge (Messing et al., 2006).

An assessment of low resolution data from NOAA National Geophysical Data Center (NOAA NGDC) integrated with sources including the U.S. National Ocean Service Hydrographic Database, U.S. geological Survey, Monterey Bay Aquarium Research Institute, U.S. Army Corps of Engineers, International Bathymetric Chart of the Caribbean Sea and the

Gulf of Mexico Project, provided a representation of the seafloor. However, this representation lacked sufficient detail to differentiate benthic habitats. High-resolution bathymetry data and biological surveys refined knowledge of the benthic habitat for this area (Messing et al., 2012).

Transect classifications for this study were adapted from previous studies (Mullins & Neuman, 1979; Messing et al., 2012; Vinick et al., 2012). The classifications in those studies were based on geomorphologic zone, substrate type, and slope. The geomorphologic zones were Inner Terrace Platform, Outer Terrace Platform, and Outer Terrace Ridge (Figure 2). The Inner Terrace Platform is the furthest inland zone. It resides in depths of roughly 235-280 m with a gradual deepening from south to north and west to east. The geomorphology of the Inner Terrace Platform is comprised primarily of low-relief substrates with some depressions of 10-m vertical relief. The Outer Terrace Platform has a depth range of 245 m – 350 m and shoals roughly ~20 m over 4.0 NM south to north. It exhibits a number of depressions, broad platforms, and ridges of up to 20 m vertical relief. The Outer Terrace Ridge has a depth range of about 300 m – 420 m exhibits scattered sinkholes and up to 20 m local vertical relief (Messing et al., 2012).

Differences in biological communities between low and high slope were notable on the Miami Terrace (Messing, 2012). Slope was categorized as high (>5 degrees) and low (≤ 5 degrees) for further analysis (Messing, 2012). The determination of geomorphologic zones in past studies was based on zones dictated by Mullins and Neumann (1979), substrate type, and slope (Vinick et al., 2012). Transects for my study were based on slope differences within the geomorphologic zones. For example, High Slope Inner Terrace transects represent the areas of high relief within the Inner Terrace platform.

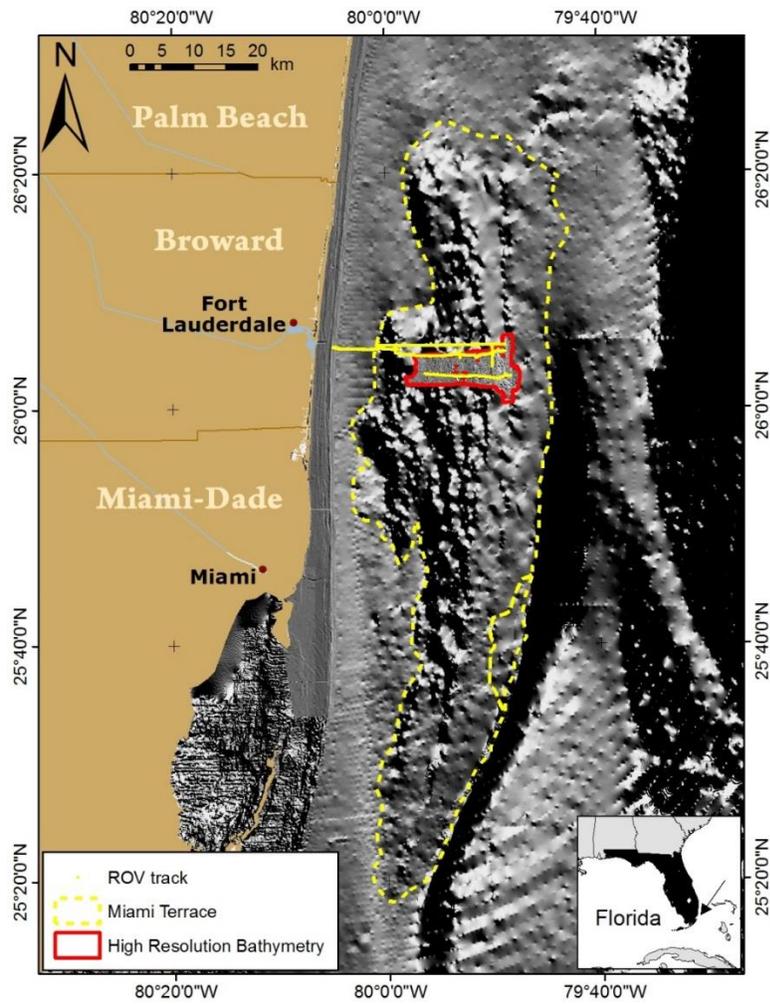


Figure 1. A map of the Miami Terrace with the entirety of the terrace outlined in dotted yellow, and the study area of high resolution bathymetry (Messing et al., 2012) outlined in red. Solid yellow lines represent the ROV tracklines. Bathymetry DEM (Reed et al., 2013)

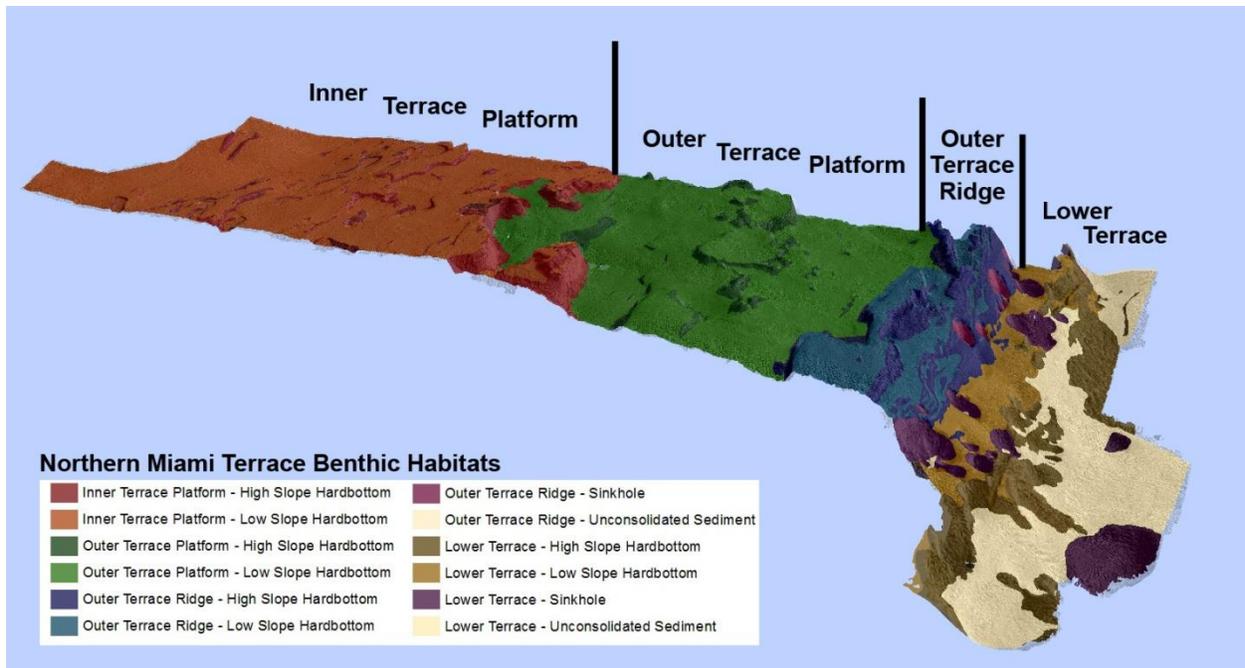


Figure 2. Map of the area of high resolution bathymetry from the Miami Terrace focused on for this study. The benthic habitats of interest to this study include the Inner Terrace Platform, Outer Terrace Platform, and Outer Terrace Ridge. (Messing et al., 2012)

Methodology

Data Collection:

The data used for this study were collected during surveys conducted for a cable impact assessment for South Florida Ocean Measurement Facility (SFOMF), and for the Department of Energy to characterize benthic habitats on the Miami Terrace. These projects included two survey lines from which still image and video were gathered. Both surveys used Naval Surface Warfare Center Carderock Division's (NSWCCD) ROV Television Observed Nautical Grappling System (TONGS) (Figure 3). See Messing et al. (2012) and Vinick et al. (2012) for details of equipment and survey methodologies.

Image Analysis:

Image analysis closely followed the protocols of Ash (2015). Suitable images were selected and grouped into transects based on location and image area. Transects were selected and characterized by depth, region, geomorphology, and bathymetric slope. Images were analyzed for percent cover of substrate, species composition and richness, and organism density.

Individual images were first reviewed, and only those with clear and focused content were selected. Those too shadowed or blurry were discarded. Those that contained relatively small shadowed or blurred areas were cropped and edited to include only the usable area. Selected images were then edited to yield the clearest and best-focused possible picture of benthic macrobiota. Most editing was carried out in Pixlr due to its accessibility as a free, open-source image-editing software. It contains a wide range of image editing capabilities comparable to those of Photoshop, which proved to be adequate for this study. Some editing was also carried out in Adobe Photoshop and Coral Point Count with Excel extensions (CPCe[®]) (Kohler and Gill, 2006) in addition to Pixlr. The most common features adjusted within an image were brightness/contrast levels.

After editing, CPCe was used to measure image area in square meters. This software uses the known distance between scaling lasers in each image to extrapolate the overall image area. Image area allowed grouping of images into transects based on the size and location of each image.

Twelve transects of ~60 m² each were chosen from the selected survey images, spaced across the survey area, and defined and named to reflect local geomorphology recognized based on multibeam mapping data. Although the survey attempted to maintain the ROV at a consistent elevation above the seafloor (between 1 and 2 m), its distance from the bottom varied, which caused image area to vary as well. Therefore, the number of images in each transect varied, but

the total area for each transect was as close to 60 m² as possible. The survey area had three distinct regions defined as the Inner Terrace Platform, Outer Terrace Platform, and Outer Terrace Ridge (Mullins & Neuman, 1979). These designations served to indicate the spatial arrangement of transects. The slope of the terrain in these areas was defined as either low or high based on 5% bathymetric slope in high-resolution multibeam data (Messing et al, 2012).

Images were analyzed in CPCe to determine percent cover of substrate and organisms. Three main substrates were defined as follows. Hardbottom (HB): definitively rocky or cemented and visibly solid substrates. Soft bottom (SB): sediment substrates (sand or mud) with no visible indication of underlying solid bottom; often rippled, lineated or bioturbated. Sediment-veneered hardbottom (SVHB): substrates covered with a sediment layer thin enough for sessile organisms to anchor, those with a recognizable indication of underlying hardbottom (e.g., surrounding small-scale protruding hard substrates), or transitional between sediment and hardbottom; sometimes difficult to distinguish.

Geomorphology was classified on the basis of slope and region on the Terrace and produced six distinct classes: High Slope Inner Terrace (HSIT), Low Slope Inner Terrace (LSIT), High Slope Outer Terrace Platform (HSOTP), Low Slope Outer Terrace Platform (LSOTP), High Slope Outer Terrace Ridge (HSOTR), and Low Slope Outer Terrace Ridge (LSOTR). Adequate images existed to create two transects for each class, as shown in Figure 3. The area of high versus low slope varied between transects, and the lack of usable images from areas of differing relief sometimes limited the number of suitable images in a transect. In particular, high slope areas yielded more dark, blurry, or otherwise unusable images, because the ROV was often too far from the bottom, or its lights created too much shadow on high-relief surfaces.

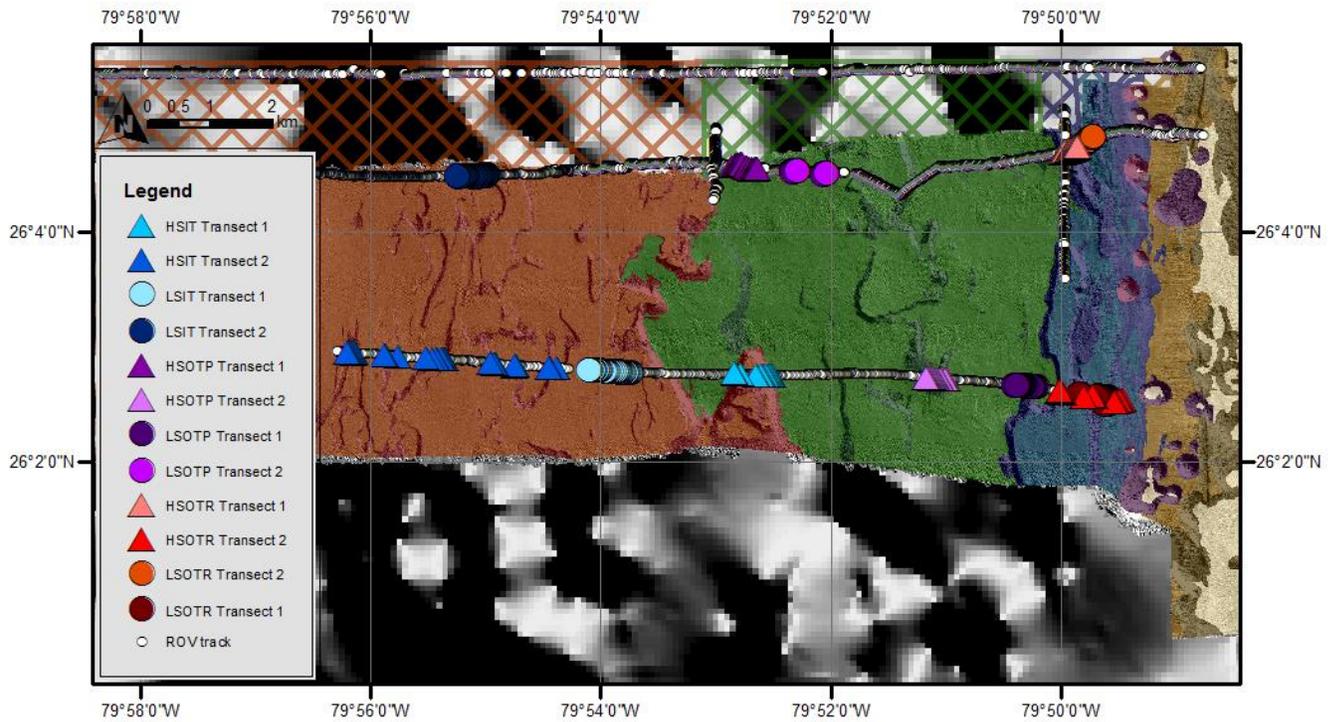


Figure 3. Multibeam map displaying the spatial arrangement of the transects analyzed in this study. Colors indicate major Terrace regions: Inner Terrace (brown), Outer Terrace Platform (green), Outer Terrace Ridge (blue/purple).

Selected transect images were then examined to identify macrobiota and determine their abundances and densities. As in previous local studies (e.g., Messing et al., 2012; Vinick et al., 2012; Ash, 2015), macrobiota were treated as all organisms greater than ~4 cm in maximum dimension, and were distinguished using calipers calibrated to half the width of the scaling lasers (8.3 cm apart) in each image. Thus, all organisms equal to or larger than this width were counted and identified to the lowest possible taxonomic level. The total number of organisms by taxon was then calculated for each transect and used to determine organism density (total number of organisms per transect divided by the total transect area in m²).

Data Analysis:

Data acquired from images and previously conducted surveys were analyzed to determine patterns in community distribution. Analyses were conducted using PRIMER v7 (Clarke and Gorley, 2006) analytical software due to its suite of multivariate statistic capabilities with particularly applicable accommodations for ecological data. PRIMER v7 was used to create a non-metric multidimensional scaling plot (nMDS) of density by transect. Analyses were performed utilizing Bray-Curtis similarity indices to determine similarities of organism densities among transects.

A cluster analysis permitted visualization of similarities among transect community composition. Non-metric multidimensional scaling was then performed to further elucidate similarity and dissimilarity among transects. Similarity Percentages (SIMPER) determined which of the organisms had the greatest effect on transect similarities. Data were square-root transformed prior to all analyses with the exception of the SIMPER test. SIMPER results were performed on unaltered density data.

Data were further explored using R Studio statistical software to determine what significant differences between organism densities at sites could be attributed to environmental factors. A One-Way Analysis of Variance (ANOVA) between transects was performed to determine if environmental factors had significant impacts on variance of variables, including the most impactful species, species richness, percent cover hard bottom, percent cover soft bottom, and organism density. Organism density was normalized to reflect that some species occur on specific substrates, while others occurred on multiple substrate types. Thus, organism density was expressed as either hardbottom organism density, soft bottom organism density, or

nondiscriminatory organism density. The most impactful species were derived from SIMPER analysis and subjected to statistical analysis in R Studio (Figure 4).

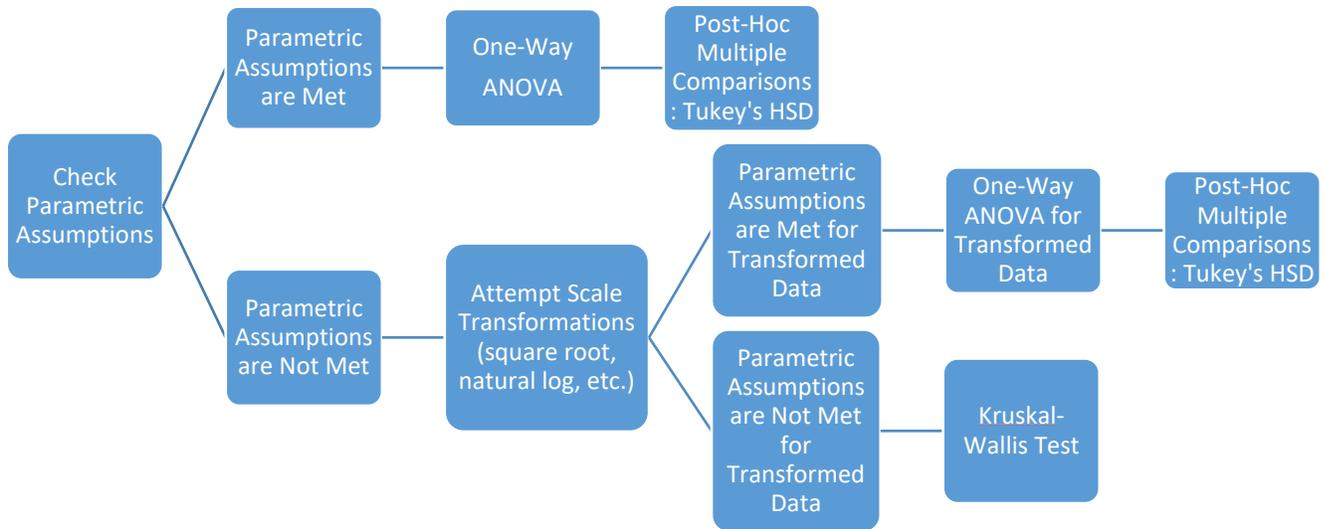


Figure 4. Flow chart illustrating procedures for statistical analyses in this study.

Analyses of Variance (ANOVA) were performed in R Studio in accordance with the guidelines set by Logan (2011), who described the general workflow for such statistical analysis. Briefly, analyses began with parametric tests to determine normality and homogeneity of variance for the data, including Shapiro-Wilk test of normality, and Bartlett's test for homogeneity of variance. If parametric assumptions were met, a One-Way ANOVA was performed. If parametric assumptions were not met, data were subjected to scale transformations. If transformed data then met the parametric assumptions, an ANOVA was performed using the transformed data. If none of the scale transformations caused the data to meet parametric

assumptions, the non-parametric Kruskal-Wallis test was performed. Rejection of the ANOVA or Kruskal-Wallis null hypothesis suggested that group means were significantly different and that the environmental factor of interest had a significant influence on group differences. Failure to reject the null hypothesis for these tests indicated no significant difference between group means. The null hypothesis was rejected if the p-value was less than 0.05. If the ANOVA null hypothesis was rejected, a Tukey's HSD post-hoc multiple comparisons test was performed to test the null hypothesis that group means were equal. A rejection of this null hypothesis further suggested that the variable was significantly affected by the environmental factor. Depending on whether parametric assumptions were met, Pearson or Spearman tests for correlation between depth or percent cover and the species driving differences across the Terrace were also performed in R Studio.

Results:

Benthic Community Density Analysis

A total of 4,092 organisms across 73 taxa were identified in the 12 transects analyzed across the study area on the Miami Terrace. Organism density, the proportion of organisms, geomorphology, depth, and substrate cover did vary across the study area. The study area shows an increase in depth across geomorphologic regions. The Inner Terrace encompasses depths from 259 m to 320 m; the Outer Terrace Platform spans a depth range of 259 m to 381 m; and the Outer Terrace Ridge exists at depths from 320 m to 442 m.

A nMDS plot illustrates the similarity of transect species densities across geomorphology with a low stress of 0.11 (Figure 5). The distribution of transect sites corresponded with terrace region (i.e. from the Inner Terrace at the lower left to Outer Terrace Platform to Outer Terrace

Ridge in the upper right). HSIT 1 visually aligns more with the Outer Terrace Platform transects, which may be due to the fact that HSIT 1 juts into the Outer Terrace Platform so it is bookended on its east and west side by areas of Outer Terrace Platform. The grouping of transects progressing from low to high slope is consistent with the exception of HSOTR 1, which appears more similar to the transects of low slope. Figure 6 shows that variations in organism densities vary with increasing depth from west to east across the terrace.

Percent cover of substrate analyzed in each image permitted identification of the dominant substrate type for each transect, referred to as the majority cover. The nMDS plot illustrates that majority cover varied across transects relative to geomorphologic region, with hard substrate dominating at most Outer Terrace sites and soft bottom (sediment) dominating at most Inner Terrace sites (Figure 7). Figure 8 illustrates ratios of percent cover by hardbottom, sediment-veneered hardbottom, soft bottom, and organism for each transect in pie charts. Majority cover, in addition to other community and environmental parameters of interest, for each transect is listed in Table 1.

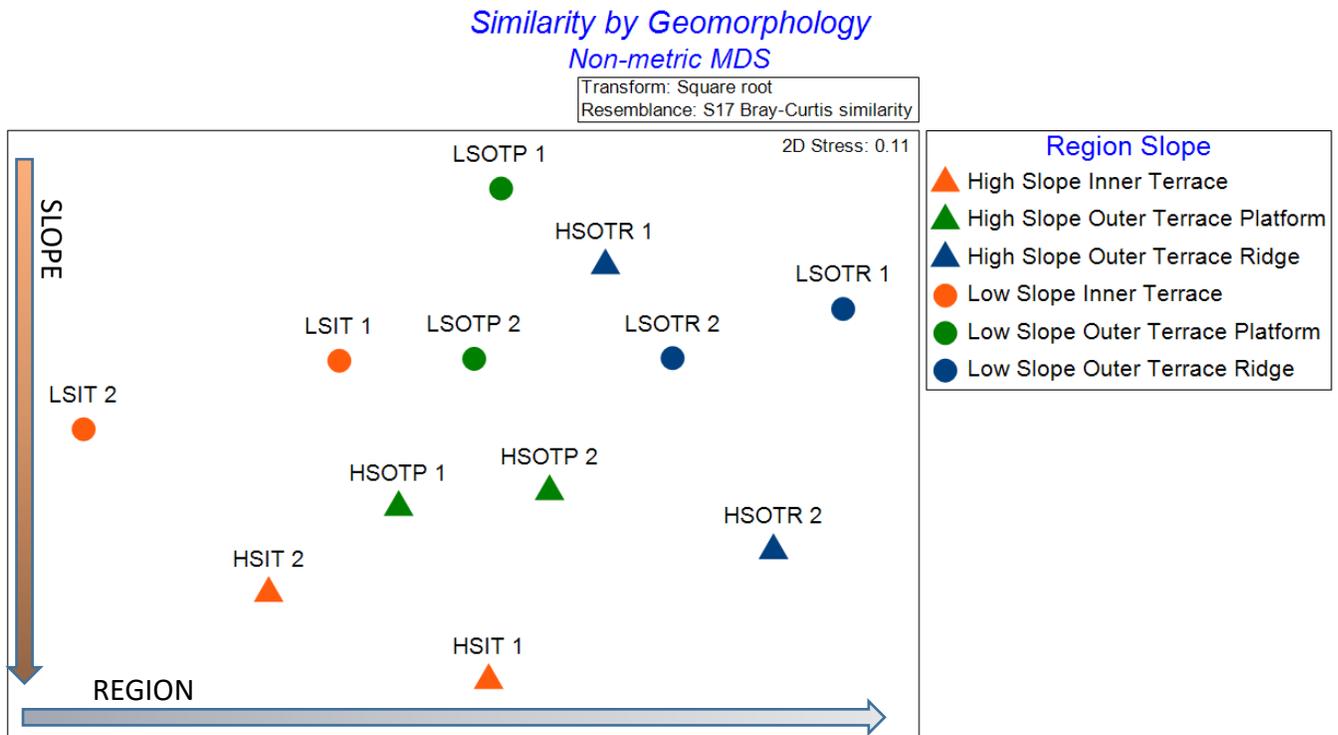


Figure 5. A nMDS plot illustrating similarity of organism densities at transects relative to geomorphologic region and slope. Progression of transects by these parameters is indicated by arrows for representing region and slope respectively.

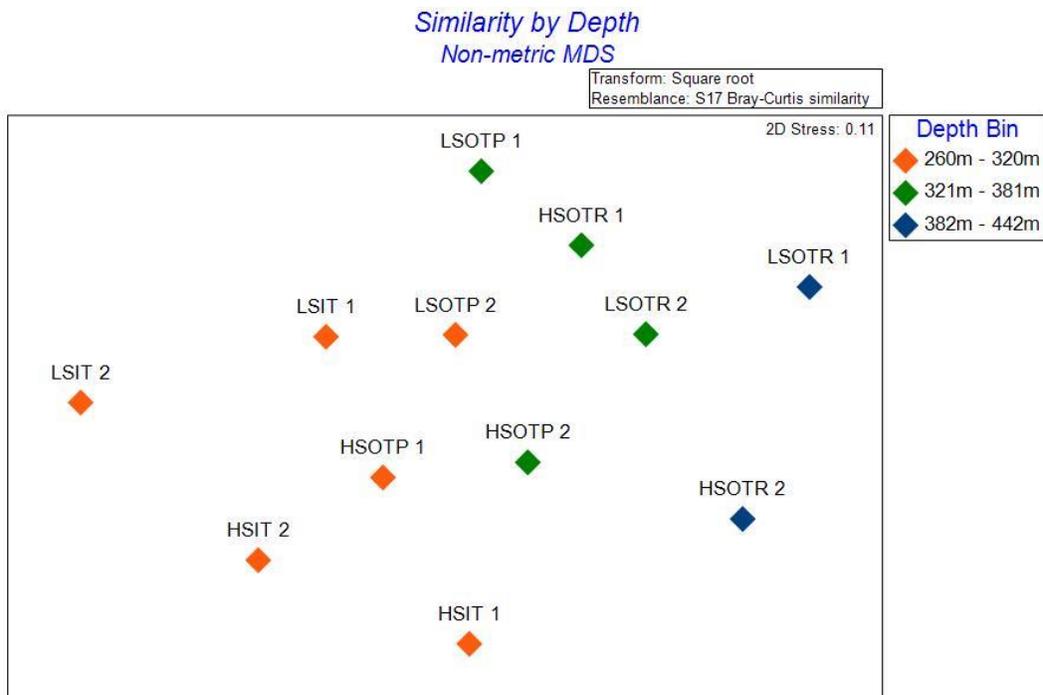


Figure 6. A nMDS plot illustrating transect species density similarity by transect relative with respect to three depth bins representing differing successively greater depth ranges.

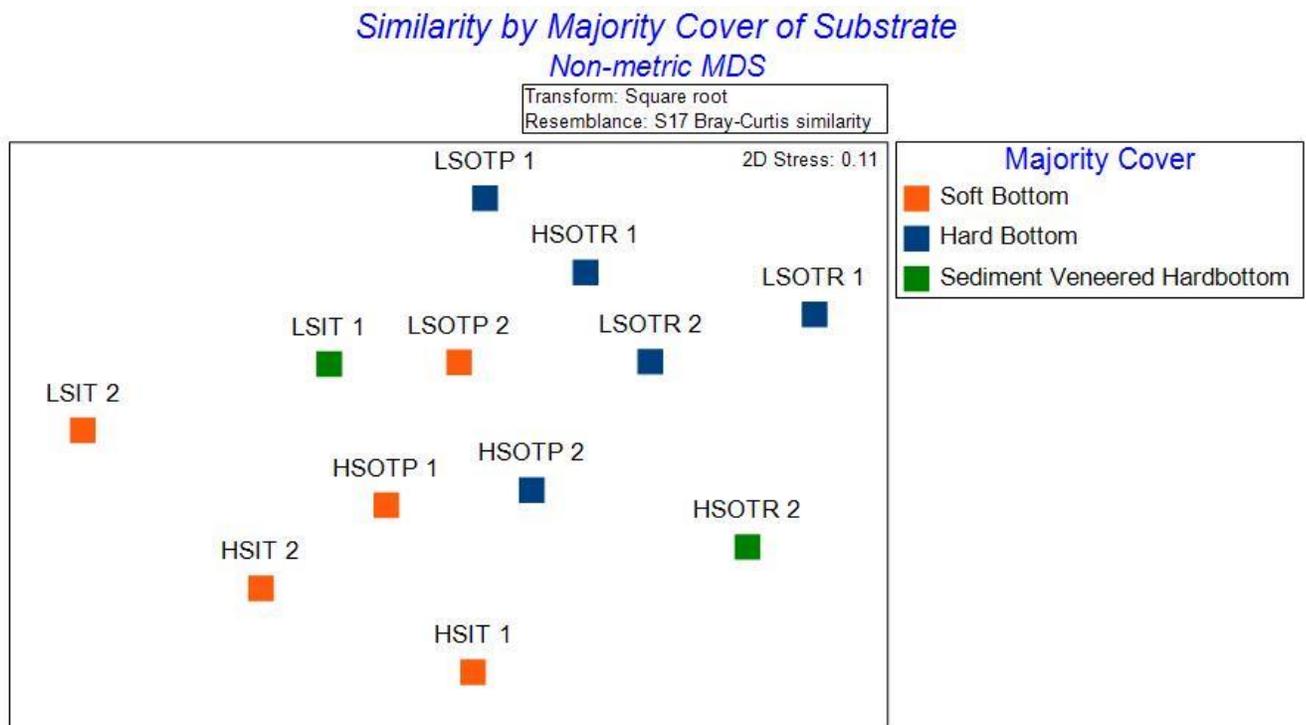


Figure 7. A nMDS plot illustrating the variance of transect species density with respect to majority cover.

Organism identification yielded 73 taxa of macrobiota identified to the lowest taxonomic level possible. Organisms were classified as preferring hardbottom or soft bottom substrates, and those organisms that inhabit both substrate types without preference were termed nondiscriminatory. Community composition by geomorphologic region as determined by SIMPER analysis revealed the species driving differences across the terrace, and is discussed below. Figure 9 overlays species contributing 75% or greater to variance between transects to the nMDS plot of transect similarity by geomorphology to visually represent the influence of these species. Cnidarians appear to group towards the Inner Terrace while poriferans have a greater density on the Outer Terrace Platform.

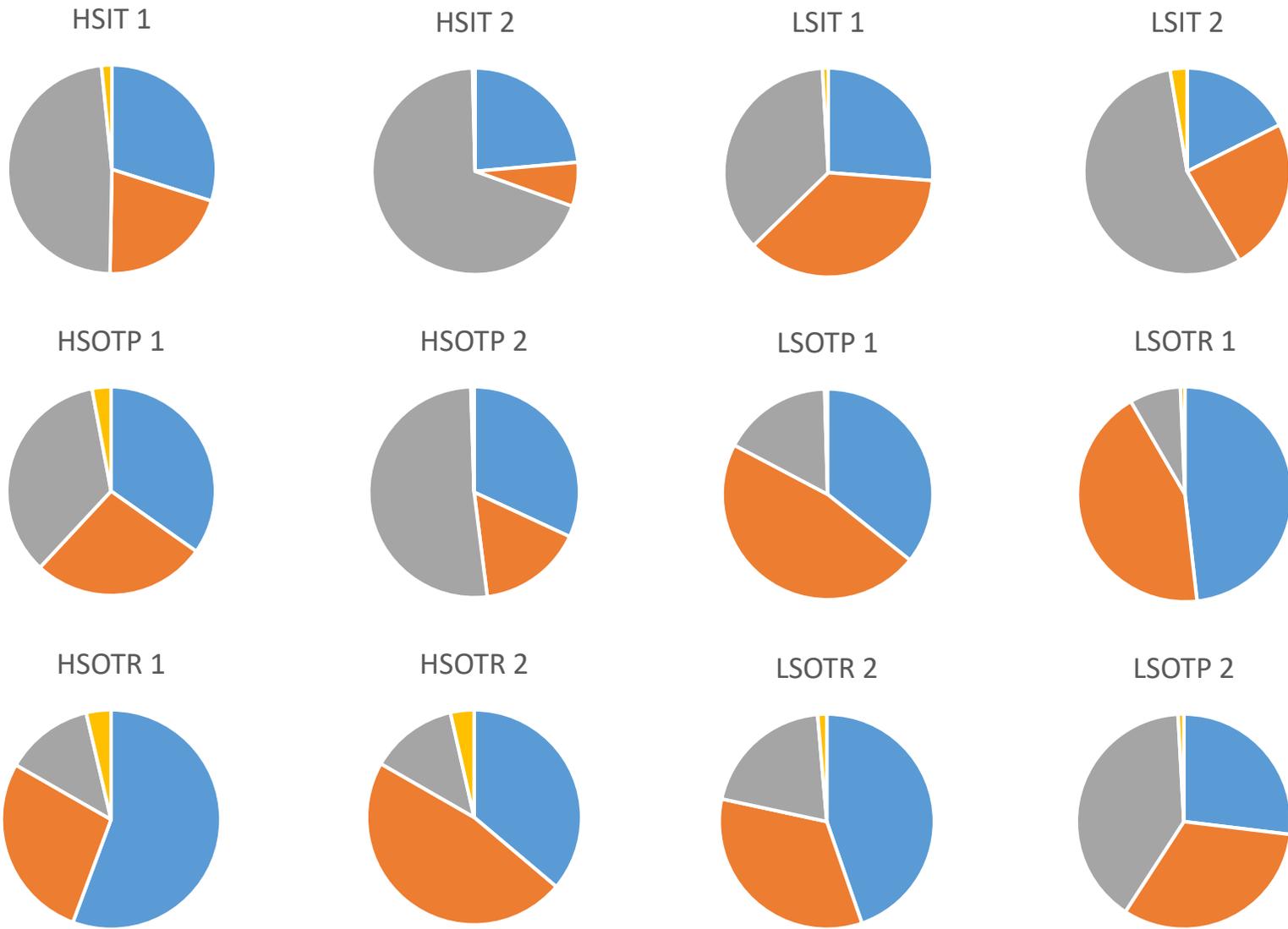


Figure 8. Pie charts for percent cover proportions of each transect. Blue – hardbottom; orange – sediment-veneered hardbottom; gray – soft bottom; yellow - organism

Table 1. Environmental parameters of interest for each transect. HB – percent cover hardbottom; SVHB – sediment-veneered hardbottom; SB – soft bottom, and ND – nondiscriminatory. Densities in numbers of organisms per m^2

Community and Environmental Details by Transect											
Transect	Transect Area (m ²)	Majority Cover	Average Depth (m)	% Cover HB	% Cover SVHB	% Cover SB	Species Richness	Overall Organism Density	HB Organism Density	SB Organism Density	ND Organism Density
HSIT 1	60	Soft Bottom	303	29.9	20.39	48.1	33	2.78	6.29	0.01	0.88
HSIT 2	60	Soft Bottom	283	23.59	6.91	69.09	29	3.21	7.34	0	1.52
LSIT 1	60	Sediment Veneered Hardbottom	272	35.72	47	16.83	24	5.89	11.65	0.01	2.82
LSIT 2	61	Soft Bottom	278	26.92	32.25	39.96	28	4.80	11.34	0.01	2.80
HSOTP 1	61	Soft Bottom	285	26.22	36.49	36.39	34	6.51	11.02	0.02	2.63
HSOTP 2	61	Soft Bottom	352	17.58	23.95	55.81	30	3.59	8.13	0.01	0.97
LSOTP 1	61	Sediment Veneered Hardbottom	363	55.67	27.61	13.06	28	7.12	12.10	0	2.79
LSOTP 2	61	Soft Bottom	290	36.15	47.15	13.15	31	9.42	25.71	0	2.50
HSOTR 1	61	Hard Bottom	333	31.92	16.08	51.5	33	10.12	14.41	0	2.09
HSOTR 2	60	Sediment Veneered Hardbottom	442	34.79	27.15	35.12	42	3.90	7.84	0	1.07
LSOTR 1	60	Hard Bottom	427	48.2	13.4	7.73	26	4.63	5.87	0	1.80
LSOTR 2	60	Hard Bottom	372	44.69	33.69	20.25	29	5.65	8.37	0	1.90

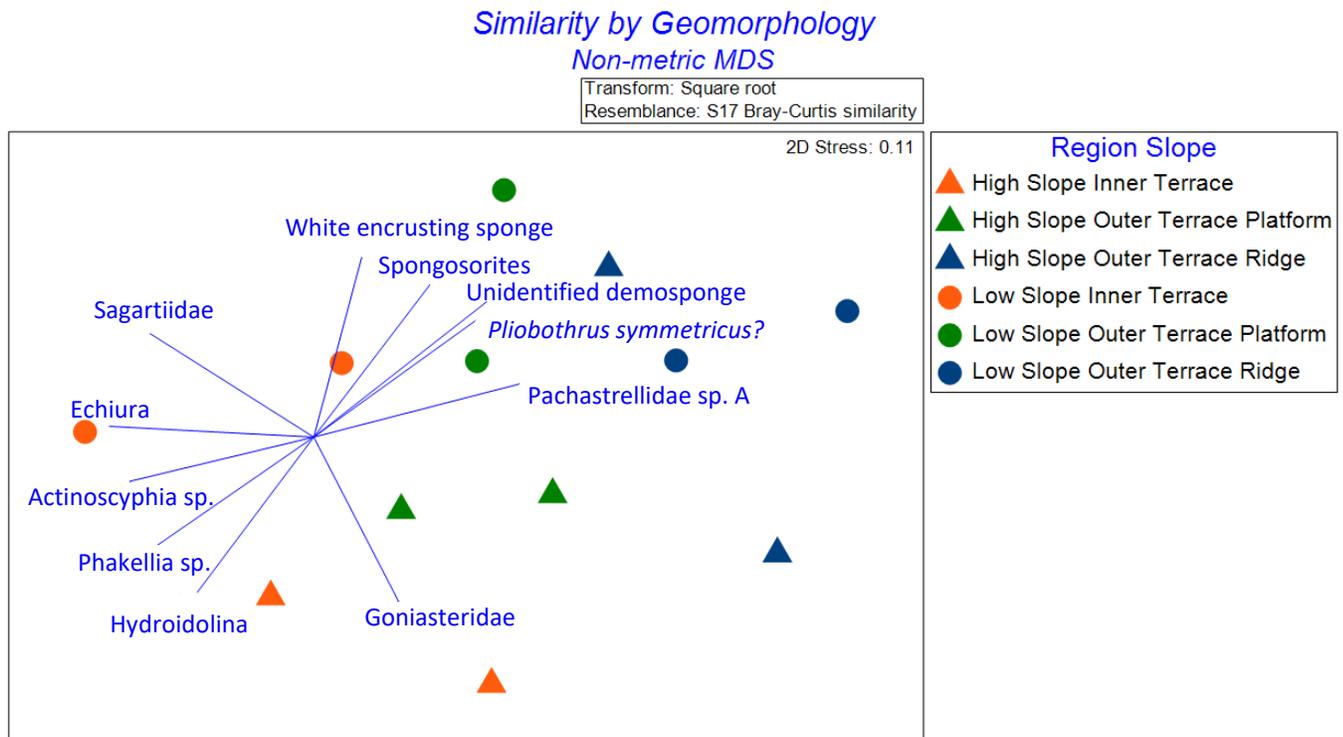


Figure 9. A nMDS plot illustrating the influence of species contributing at least 75% to variance in transect similarity. Transects are spatially arranged as in Figure 5.

SIMPER Results:

The species selected for analysis in SIMPER contributed at least 5% to community differences within or between transects. All species shown in Figure 9 to be driving differences across the Terrace also contributed at least 5% to community differences as determined by SIMPER analyses. These most important species were then subjected to One-Way ANOVA and Post-Hoc multiple comparison tests in R Studio to determine whether species density differed significantly relative to geomorphology. The average density of these species across the geomorphologic classes of the Miami Terrace is outlined in Table 2.

Table 2: Average density of the most important taxa across geomorphologic regions and with substrate preference of each taxa. Density is shaded light to dark from lowest to highest density for each taxon to visually demonstrate trends.

Variance of Average Organism Density Across Geomorphologic Classes for Most Impactful Species							
Species	HSIT	LSIT	HSOTP	LSOTP	HSOTR	LSOTR	Substrate Preference
Actinoscyphia sp. (Venus flytrap anemone)	3.5	7	3.5	6	0	0	hardbottom
Astrophorida	4	4.5	0.5	13.5	10.5	12	hardbottom
<i>Pliobothrus symmetricus?</i> (Blunt tipped stylasterid)	2	3.5	6.5	23	19.5	23.5	hardbottom
Hydroidolina (Bottlebrush hydroid)	4	1	1	0	0.5	0	hardbottom
Stylasteridae (Dense white stylasterid)	2.5	0.5	3.5	1	20	8.5	hardbottom
Echiura	6.5	30.5	12	5	3.5	1	Nondiscriminatory
Goniasteridae	0.5	0	0	0	0.5	0	Nondiscriminatory
<i>Liponema</i> (Pompom anemone)	7	32	8.5	22.5	1	5	Nondiscriminatory
Ophiuroidea	51.5	81	65	99.5	57	73.5	Nondiscriminatory
Pachastrellidae sp. A	4.5	2	6.5	7.5	8.5	15.5	hardbottom
Phakellia sp.	1	1	0	0	0	0	hardbottom
Sagartiidae (Pink lip anemone)	2	6.5	2	8.5	2.5	0	hardbottom
<i>Plumarella pourtalesii</i>	4.5	0.5	13.5	1.5	25	8	hardbottom
<i>Pseudodrifa nigra</i>	26	44.5	27.5	47.5	18.5	1	hardbottom
Unidentified demosponge	0	0	0.5	5.5	10.5	15	hardbottom
White encrusting sponge	4.5	18	11	34.5	16	19.5	hardbottom
Spongosorites (Yellow encrusting sponge)	0	0	0	0.5	0.5	1.5	hardbottom

Analyses of variance were performed for geomorphologic region as well as slope to elucidate the impact of geomorphology on species distribution. The results of those and other statistical analysis performed for the factors of region, slope, depth, and percent cover follow.

Analysis by Region

Analysis of Variance by Region

Table 3 shows the results of ANOVAs and Kruskal-Wallis tests for those species that varied significantly by region. It is evident that geomorphologic region affects the distribution of some species more profoundly than others. For example, the dense white stylasterid and blunt-tipped stylasterid have much lower p-values than Phakellia sp. or Liponema sp. Pachastrellidae sp. A also had a comparatively low p-value ($p < 0.01$; df: 2). The variables that exhibited the most significant variance by geomorphologic region were percent cover hardbottom and soft bottom with p-values of 0.0019 and 0.0041, respectively. Correlations between percent cover and species distribution are explored further below. ANOVAs for the dense white and the blunt tipped stylasterid yielded appropriately low p-values of 0.007 and 0.016 respectively. They were then analyzed by post-hoc multiple comparisons to further define their variance across geomorphology.

Table 3. Results of One-Way ANOVA or Kruskal-Wallis test by region.

One-Way ANOVA by Region				
Variable	Parametric Assumptions Met	Scale Transformation	Test Performed	P-value
<i>Pliobothrus symmetricus?</i> (Blunt tipped stylasterid)	Yes	-	ANOVA	0.01615
Stylasteridae (Dense white stylasterid)	No	square-root	ANOVA	0.007303
<i>Liponema</i> (Pompom anemone)	No	-	Kruskall-Wallis	0.04467
Pachastrellidae A	No	-	Kruskall-Wallis	0.00938
<i>Phakellia</i>	No	-	Kruskall-Wallis	0.02732
Unidentified demosponge	No	-	Kruskall-Wallis	0.01472
Percent cover hardbottom	Yes	-	ANOVA	0.001927
Percent cover soft bottom	Yes	-	ANOVA	0.004103

Table 4 shows the results of Tukey’s HSD test. The density of the blunt-tipped stylasterid on the Inner Terrace is significantly different from both the Outer Terrace Platform and Outer Terrace Ridge with $p= 0.05$, although it did not vary significantly from the Outer Terrace Ridge to Outer Terrace Platform. Table 2 shows that the average density of the blunt-tipped stylasterid more than tripled on the Low Slope Outer Platform and Outer Terrace Ridge relative to the Inner Terrace, whereas average density of the dense white stylasterid was significantly greater only on the Outer Terrace Ridge.

Table 4: Results of Tukey’s HSD test performed on species subjected to One-Way ANOVA and whose p-values suggested significant variance of density across regions. Regions are abbreviated as OTP (Outer Terrace Platform), IT (Inner Terrace) and OTR (Outer Terrace Ridge). Significant difference in average density between regions is denoted by an asterisk (*).

Tukey's HSD Test by Region			
Species	OTP-IT	OTR-IT	OTR-OTP
<i>Pliobothrus symmetricus?</i> (Blunt tipped stylasterid)	0.037558*	0.004435*	0.372342
Dense white stylasterid	0.921644	0.010014*	0.01799*

Analysis by Slope

Analysis of Variance by Slope

Table 5 lists the results of analysis of variance by slope for those species that varied significantly. *Plumarella pourtalesii* yielded a significant p-value of 0.049, while the variance in density of the white encrusting sponge and ophiuroids also varied significantly (p-values 0.021 and 0.032, respectively). Species richness was significantly different between high and low slope (p-value 0.02).

Table 5. Results of One-way ANOVA or Kruskal-Wallis test by slope.

One-Way ANOVA by Slope				
Variable	Parametric Assumptions Met	Scale Transformation	Test Performed	P-value
Ophiuroidea	Yes	-	ANOVA	0.03215*
<i>Plumarella pourtalesii</i>	No	square-root	ANOVA	0.04914*
White encrusting sponge	Yes	-	ANOVA	0.02146*
Nondiscriminatory org dens	No	-	Kruskall-Wallis	0.03737*
Species richness	Yes	-	ANOVA	0.02042*

Post-Hoc Multiple Comparisons by Slope

Tukey's HSD test by slope revealed significant trends in species density relative to slope for Ophiuroidea, *P. pourtalesii*, and the white encrusting sponge (Table 6). Ophiuroidea and the white encrusting sponge appeared at significantly higher densities in low slope areas (p value 0.0032 and 0.021, respectively), whereas *P. pourtalesii* consistently exhibited higher densities in high slope areas (p-value <0.05) (Table 2). Trends in overall species richness were significantly different between areas of high and low slope. Species richness yielded a p-value of 0.02 and can be seen to be greater in areas of high slope (Table 1).

Table 6: Results of Tukey's HMC test performed on species subjected to One-Way ANOVA with p-value suggesting significant variations in density between areas of high versus low slope. Significant difference in average density based on slope is denoted by an asterisk (*).

Tukey's HSD Test by Slope	
Ophiuroidea	0.032151*
<i>Plumarella pourtalesii</i>	0.04914*
White encrusting sponge	0.021458*
Species richness	0.020424*

Characterization of Transects

Depth, substrate cover, species richness, and organism density all exhibit distinct trends relative to geomorphology across the Miami Terrace (Table 1). Species richness increased with depth from the Inner Terrace to the Outer Terrace Ridge, accompanied by a shift from a majority substrate composition of soft bottom to hardbottom. The density of soft bottom organisms was higher on the Inner Terrace and Outer Terrace Platform than on the Outer Terrace Ridge. Similarly, the Outer Terrace Platform and Outer Terrace Ridge exhibited greater hardbottom organism densities than the Inner Terrace. However, LSOTP 2 had the highest hardbottom organism density of all transects. Overall organism density was typically lower on the Inner

Terrace than on the Outer Terrace Platform or Ridge. Overall organism density reached its peak on the outer terrace in HSOTR 1.

Transects LSIT 2, LSIT 1, HSIT 1, and HSOTP 1 lie sequentially from west to east and supported the highest densities of organisms that prefer soft bottom habitats. HSOTP 2 was the only other transect with soft bottom preferential organisms present. These transects exhibited similar substrate cover and depth. Soft bottom dominated at all of these except LSIT 1. LSIT 2, LSIT 1, and HSOTP 1 existed at similar depths and supported similar organism densities, with LSIT 2 and LSIT 1 most similar. Results of correlation tests to elucidate which, if any, species correlated with substrate cover or depth are given in Table 7-9, below.

Correlation Between Organism Density and Percent Cover or Depth

The variations in percent cover of hardbottom and soft bottom across the transects correlated with Cnidaria as well as Porifera (Tables 7 and 8). Percent cover soft bottom had a strong negative correlation with the yellow encrusting sponge (-0.629), unidentified demosponge (-0.732), Pachastrellidae sp. A (-0.697), dense white stylasterid (-0.5828), and blunt tipped stylasterid (-0.64). Percent cover soft bottom correlated positively with the bottlebrush hydroid (0.6502). On the Inner Terrace, where soft bottom dominated, cnidarian density was greater than that of sponges, whereas sponges became more dominant further east where percent cover hardbottom increased.

Percent cover hardbottom correlated with a greater number of species, and those correlations were typically stronger than correlations between percent cover soft bottom or depth. Percent cover hardbottom correlated strongly and positively with the yellow encrusting sponge (0.719), unidentified demosponge (0.854), *Plumarella pourtalesii* (0.6058), Pachastrellidae sp. A (0.716), and the dense white stylasterid (0.796). Notable negative

correlations existed between hardbottom and Phakellia sp. (-0.621) as well as Actinoscyphia sp. (-0.670). Table 9 indicates that depth correlated negatively with the distribution of Actinoscyphia sp. (-0.729) and *Pseudodrifa nigra* (-0.711), but positively with Pachastrellidae sp. A (0.74).

Table 7-9. Results of Pearson's correlation test between density of organisms and percent cover soft bottom, percent cover hardbottom, and depth respectively.

Correlation between Percent Cover Soft Bottom and Organism Density		Correlation between Percent Cover Hardbottom and Organism Density		Correlation between Depth and Organism Density	
Organism	R-value	Organism	R-value	Organism	R-value
Yellow encrusting sponge	-0.629	Yellow encrusting sponge	0.719	Actinoscyphia sp. (Venus flytrap anemone)	-0.729
Unidentified demosponge	-0.732	Actinoscyphia sp. (Venus flytrap anemone)	-0.67	<i>Pseudodrifa nigra</i>	-0.711
Pachastrellidae sp. A	-0.697	Unidentified demosponge	0.854	Pachastrellidae sp. A	0.74
Stylasteridae (Dense white stylasterid)	-0.5828	<i>Plumarella pourtalesii</i>	0.6058		
Hydroidolina (Bottlebrush hydroid)	0.6502	Phakellia	-0.621		
<i>Pliobothrus symmetricus?</i> (Blunt-tipped stylasterid)	-0.64	Pachastrellidae sp. A	0.716		
		Stylasteridae (Dense white stylasterid)	0.796		

Discussion

Community Analysis

This study supports that geomorphologic region, slope, depth, and percent cover of substrate significantly affect the Miami Terrace benthic community structure and thus can be useful as surrogates to determine different deep-water habitats. This is consistent with previous

research that has shown that geomorphology impacts community differences on the Pourtalès Terrace and deep-water reefs off the eastern coast of Florida (Shirur, 2008; Ash, 2015); and it is consistent with widespread findings that the distribution of benthic assemblages is influenced by geomorphology (Wilson et al., 2007; Harris, 2012). A significantly higher species richness on high slope areas is consistent with observations that deep-sea benthic macrofaunal communities associate with high-relief geologic features (Reed et al., 2014); e.g., a greater number of species occurred on the high slope Outer Terrace Platform and Outer Terrace Ridge than in the low slope areas.

The increase in depth across the Terrace towards the Outer Terrace Ridge likely contributed to species distributions. Ash (2015) found that, on the Pourtalès Terrace, depth and location (region) were chief drivers of community differences. In that study, transects separated into five bins based on location and depth (e.g., West 150-300, North Central 150–250, Central 250–300, South 450–500, and South 500-550; numbers refer to depths in meters) provided the clearest indication of different benthic communities.

For my assessment of the Miami Terrace, depth was addressed independently rather than in combination with location. Depth did not significantly affect variations in total organism density on the Miami Terrace, but it did correlate with the density of a number of species (table 9). This is consistent with the tendency for depth to covary with environmental factors that directly impact species distribution rather than depth itself being the driver of distribution (Harris and Baker, 2012). The nMDS plot for similarity of benthic community densities (Figure 6) by depth shows that transects within the same depth bin cluster more closely than those of different depth bins with the exception of LSOTP 1. Some transects from depth bin 260-320 m group

more closely with those of depth bin 321-381 m. Depth bin 382-442 m can be seen to group away from the other depth bins.

Although depth did not significantly affect total organism density, it was significant for certain species, e.g., the venus flytrap anemone, *P. nigra* soft coral, and Pachastrellidae sp. A. Although the density of these organisms did not vary significantly by geomorphology, the density of Pachastrellidae sp. A increased towards the Outer Terrace Ridge. Conversely, densities of Actinoscyphia sp. (the venus flytrap anemone) and *P. nigra* were drastically reduced on the Outer Terrace Ridge. This is consistent with how Porifera and hard corals, such as the stylasterids, drive differences towards the Outer Terrace (Figure 9) while anemones and soft corals, such as *P. nigra*, are more abundant and drive differences between transects of the Inner Terrace.

Quality of substrate (i.e. whether the substrate is hardbottom, softbottom, etc.) can affect species distribution (Kostylev, 2001; Wilson et al. 2007; Harris and Baker, 2012). All of the species driving community differences on the Miami Terrace either preferred hardbottom habitats or were nondiscriminatory in nature, which suggests that the availability of hardbottom habitats affects the density of those organisms. For example, the blunt-tipped stylasterid and dense-white stylasterid became more abundant towards the Outer Terrace Ridge. Additionally, *Liponema* sp., Pachastrellidae sp. A, *Phakellia* sp., and unidentified demosponge varied significantly across the geomorphologic regions. Each prefer hardbottom, and most become more densely populated towards the Outer Terrace Ridge. The only exception to this is *Phakellia* sp., which was only found on the Inner Terrace in this study. However, Reed (personal communication) recorded it on the Miami Terrace escarpment, although the possibility exists that this might be a different species. Shirur (2008) found that sponges on deep-water reefs off

eastern Florida correlate with higher concentrations of hardbottom substrate. Ash (2015) also found percent cover of substrate influenced the distribution of species, including sagartiid anemones and several species of stylasterid corals, across the Pourtales Terrace.

Overall organism density, in particular that of stylasterids and sponges, increased towards the Outer Terrace Ridge and its corresponding increase in hardbottom habitat. For example, most sponges occurred on the Outer Terrace Ridge. This was consistent with results from studies conducted off the Florida coast by Ash (2015) and Reed (2012), who reported finding hardbottom areas dominated by Porifera and Cnidaria, particularly stylasterids. Hardbottom habitats are known to influence the distribution of many organisms (Harris and Baker, 2011); and the higher organism density of hardbottom areas reflects the influence of species in this study who prefer hardbottom habitat, such as the stylasterids.

In addition to the abundance of hardbottom habitat potentially influencing the distribution of species since many of the species in this study prefer hardbottom habitat, near-bottom flow on the Outer Terrace Ridge is likely more suitable for corals such as stylasterids and other suspension feeders (Harris and Baker 2012). Shirur (2008) noted that both the stony coral, *Lophelia pertusa*, and stylasterid-dominated areas occurred in higher abundance along the escarpment of the Miami Terrace in association with higher current velocities. Additionally, Messing et al. (1990) noted deep-water coral reef structures orient to local currents in the Straits of Florida. All these findings suggest that currents are important to consider when assessing the distribution of corals such as stylasterids and octocorals including *P. pourtalesii* on the Miami Terrace.

The nuanced interactions between the different components of geomorphology and the environmental preferences of organisms make it difficult to determine the efficacy of

geomorphology as a surrogate. It is difficult to account for all of the environmental variables (such as currents, substrate cover, major geologic features, slope, and depth) that could be influencing the community composition of an area. As relatively little is known about the distribution and preferences of the great majority of deep-sea organisms, identifying an effective surrogate is complicated (Costa et al., 2018). As environmental factors such as depth and substrate can co-vary, it can be difficult to distinguish which influences species distribution, either directly or indirectly (Harris, 2012; Costa et al., 2018). For example, *Phakellia* sp. was absent from the Outer Terrace Platform and Ridge despite the increased proportion of hardbottom; this suggests that a different, unknown, environmental factor limits its distribution.

Harris (2012) found that certain environmental factors, such as substrate and depth, integrated into geomorphology are the best predictors of distribution at the species level. This suggests that no single environmental factor can serve as a completely reliable surrogate for benthic community structure. This is also the case on the Miami Terrace, except that when the significantly affected species comprise a large portion of the benthic population, the entire community shifts with changing factors like depth and relief, even though relatively few species statistically varied by geomorphology. There are almost certainly other factors that would be better predictors of species distributions in many cases that are not related to our geomorphologic classifications, however significant differences in benthic communities were found to vary across these factors that are relatively easy to capture remotely from multibeam bathymetry. It is the relative ease with which these environmental factors can be determined that makes them highly valuable as surrogates despite their limited predictive capacity.

Surrogacy bears an inherent level of uncertainty. The complexity of marine ecosystems can confound the usefulness of seemingly robust environmental surrogates. That is, direct

observation may reveal a benthic habitat different than the one anticipated by an environmental surrogate due to the influence of an environmental factor that was not considered. Additionally, the influence of specific environmental factors varies across space and by species, and the parameters used to distinguish geomorphological features vary among studies. Geomorphology can be defined as broadly as general geomorphic features, or can include details such as sediment grain size depending on the ecological relevance and intended application of the study (Harris, 2012).

Since Ash (2015) did not directly address slope from multibeam data in her classification when assessing the Pourtalès Terrace, the impact of slope on species distribution in that study area remains unknown. Slope was an integral component of geomorphologic classification for the Miami Terrace and affected species distributions. Slope proved to be significantly tied to the density of certain organisms including the white encrusting sponge, ophiuroids, and *P. pourtalesii*. These discrepancies in definition can make meaningful comparisons between studies difficult. For example, Ash (2015) used the specific geologic feature (e.g., valley, mound-slope, mound-wall, mound-top, deep-mound) as geomorphology, instead of separating slope from geomorphologic features. That both of these studies found geomorphology to have different degrees of influence on the distribution of species could be due to the different components of geomorphology addressed in these respective studies, or could simply be representative of geomorphology impacting distribution differently on the Pourtalès Terrace than on the Miami Terrace.

A pressing need exists to explore and characterize deep-sea habitats because such a small percentage of deep-sea resources have been investigated, and deleterious influences to deep-sea habitats (e.g., mining, bottom trawling, traps, over-fishing) threaten severe damage to unknown

deep-sea communities (Ross, 2004; Roberts et al., 2006; Robinson, 2009; NOAA, 2015). A large portion of benthic habitat studies to date operate on a fine scale ($<1\text{m}^2$), which leaves large gaps in our knowledge of benthic habitats (Costa et al., 2018). Since the direct observation of deep-sea benthic habitats is often logistically prohibitive, a surrogate is necessary to establish a baseline to meet the need for management of deep-sea resources. The research into the efficacy of using geomorphology as a surrogate is still in development, and many studies that suggest that geomorphology affects species distribution did not perform the statistical analyses required to verify that relationship. Stevens et al. (2004) investigated the efficacy of abiotic variables as predictors for species distribution in Moreton Bay, Australia, and found that the most robust surrogate was driving less than 30% of biological similarity, and questioned the utility of abiotic surrogates in designing marine protected areas. Although Walker (2012) noted that surrogacy is more effective at finer scales, geomorphology is nevertheless useful for establishing baseline information for benthic habitats.

The vast percentage of deep-sea habitats lack the baseline information that can be used for resource management applications such as fisheries management, offshore infrastructure development, establishment of reserves and protected areas, tourism, and comprehensive general knowledge of marine resources (Tittensor et al. 2010; Harris, 2012). Our ability to map areas exceeds our ability to sample and explore those areas, and this can lead to the misrepresentation of habitats (i.e., an area could appear to be ideal for certain species, but be found to be void of organisms upon exploration). Harris (2012) found that the use of abiotic surrogates often leads to overestimating the distribution of species. As such, direct observations and surveys of deep-sea habitats are needed to describe deep-sea components; although, environmental surrogates are useful tools for guiding such explorations.

Although the relationship between geomorphology and community composition is only beginning to be understood, studies worldwide (including this one) are finding relationships between the distribution of species and one or more components of geomorphology (Harris, 2012). Because the influence of geomorphology on species distribution varies, its predictive capacity and efficacy as a surrogate remains limited. Still, the need for predictive models to guide management decisions and establish ecological baselines outweighs the uncertainty associated with a surrogate such as geomorphology (Robinson, 2009; Huang et al., 2011; Ross et al. 2012). Geomorphology as defined herein had limited significant influence on species distributions. However, a more detailed treatment of geomorphological attributes, e.g., substrate quality and patterns of near-bottom flow, together with region and slope might better reflect species distributions on the Miami Terrace and elsewhere. Further research into the nuanced effects of the factors determining species distributions, and how they relate to geomorphology, will better define its usefulness as a surrogate.

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