

**DISTRIBUTION AND DIVERSITY OF OCTOCORALS  
IN THE GULF OF MEXICO**

A Dissertation

by

PETER J. ETNOYER

Submitted to the Office of Graduate Studies of  
Texas A&M University- Corpus Christi  
In partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August, 2009

Major subject: Coastal and Marine System Science

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## ABSTRACT

Distribution and Diversity of Octocorals in the Gulf of Mexico

August, 2009

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Octocorals are broadly distributed throughout the world's oceans, from the shallow intertidal zone to deeper than 5800 meters. Fishermen refer to large colonies as 'trees'. This is appropriate because colonies provide complex structural habitat for associated species, they are broadly distributed, and they are threatened by industrial practices, such as bottom trawling. Below the warm water layer (50 – 70 m deep), octocorals are presumed to be cosmopolitan in the West Atlantic, with a broadly homogenous distribution. This creates a problem for conservation and management because it is difficult to justify conservation of one place, if all others are the same.

This dissertation tested the null hypothesis of no difference in octocoral assemblages at the three spatial scales (referred to as basin, region, and site scale) through meta-analysis of two large, original datasets. The first was 1881 records of octocoral occurrences in the Gulf of Mexico from cruise reports and museums. The second was 8495 seafloor images from six outer continental shelf banks, and one site between banks, in the northwestern Gulf region. Univariate, multivariate, and spatial analysis techniques were used to compare genera, depth zones, regions, and banks within a Geographic Information System framework.

Octocoral assemblages in the Gulf of Mexico differed significantly between depth zones and regions, but there was no difference in diversity between depth zones less than 800 m, due to species replacement. Composition of octocoral assemblages varied significantly between sites, and hotspots for richness and abundance were evident within sites. Null hypotheses of no difference between banks, depth zones, and regions were rejected with confidence. The findings support the broad distribution of octocorals in the Gulf of Mexico, but not homogeneity of octocoral assemblages. Based on these results, place-based conservation of deep octocoral habitat is justified, because some sites have higher diversity and abundance of octocorals than others.

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## DEDICATION

This dissertation is dedicated to my Family; for their encouragement and support, especially to my wife, Maria, and to my children, Clara Lynn and Ana Rose, who worked and played around me while I sat typing at a little white desk, in the kitchen-corner, for two years. Thanks to my mother, Mildred Böressen and my father, John Etnoyer, who set me on this path, and encouraged me. Special thanks to my extended family for their faith and kindness; and to my sisters, Kirsten and Erika, and to my brothers Franz, Rodrigo, Fred, Chad, Bill, and Michael, as we all work to build our families together.

## INTRODUCTION

Octocorals (Anthozoa: Alcyonaria:) are common and conspicuous coral reef fauna in the shallow Gulf of Mexico and Caribbean Sea (Cairns 1977), but they occur worldwide deeper than 5800 m (Cairns & Bayer 2009). Most octocoral species occur in deep water (Cairns 2007a), but the majority of what is known about the forces structuring octocoral communities is from shallow coral reef literature. Octocorallia are listed among the suspension feeding benthic megafauna, but the subclass is speciose, and well adapted to a broad variety of oceanic conditions.

Within any given study site, different octocoral assemblages can be distributed along a continuum of environmental conditions (Sanchez et al. 1997). Depth, particle flux, productivity, wave exposure, hard substrate exposure, and periodic disturbance structure the octocoral community (Bayer 1961, Peccini & MacDonald, Lasker & Coffroth 1983, Yoshioka & Yoshioka 1987, 1991). Competition is a structuring agent. There is an inverse relationship between zooxanthellate hard coral cover and soft cover (Kinzie 1970). Abundance of autotrophic octocorals diminishes with light. Heterotrophic octocorals lack zooxanthellae, relying on the plankton for their nutrition. They are found dispersed along the edges of reefs, where planktonic resources are not depleted by suspension feeders (Sanchez et al. 1998, Sanchez 1999, Fabricius & De'ath 2008).

Deep-water octocorals are heterotrophic, broadly distributed on continental slopes and seamounts throughout the world's oceans (Bayer 1956, Rogers et al. 2007), occurring deeper than 5800 m (Cairns & Bayer 2009) wherever suitable substrate exists. Deep-sea gorgonians are long lived (Andrews et al. 2002, Roark et al. 2005). They create complex structure in a relatively featureless environment, generating habitat for associated species

of microbial fauna (Penn et al 2006), invertebrates (Krieger & Wing 2002, Buhl-Mortensen & Mortensen 2005), and fish (Heifetz 2002, Etnoyer & Warrenchuk 2007). Gorgonian assemblages are presumed to provide refuge and substrate to commercially important species, and were included in the recent reauthorization of the Magnuson-Stevens Fisheries Conservation Act. Still, there is limited knowledge of the character and extent of deep-water octocoral habitats in most ocean basins.

Deep-water octocoral distribution in the Gulf of Mexico is well studied compared to other basins, one of the few ocean basins with an iterative octocoral inventory that dates to the 19<sup>th</sup> century (Verrill 1883, Agassiz 1888, Deichmann 1936, Bayer 1954, 1957, 1961, Cairns & Bayer 2009). Giammona (1978) provided a review of Gulf of Mexico research cruises and expeditions that dredged octocorals. Since the early 1970's researchers have employed manned submersibles (Rezak et al. 1978, Reed et al. 2005, 2006) and remotely operated vehicles (Gittings et al. 1992, this study) to characterize living octocoral habitat and to collect new samples. Taxonomic revisions are ongoing through a series of manuscripts dedicated to west Atlantic Octocorallia (Cairns & Bayer 2004, Cairns 2006, 2007b, 2007c, and others) but several fairly common genera (e.g., *Acanella*, *Thesea*, *Placogorgia*) are still in need of revision (this study).

Bayer (1961) considered deep-water octocorals in the Gulf of Mexico to be a broadly cosmopolitan assemblage typical of the West Atlantic. This was supported by empirical studies (Giammona 1978). Though Bayer found no evidence of regionalization in deep water, he identified factors limiting octocoral distribution, including high temperature (Cary 1914) and soft substrates (Bayer 1961). A study of gorgonian distribution along a submarine canyon in Atlantic Canada identified seven environmental

factors that explained the variation in octocoral composition. Of these, four were related to substrate, one to salinity, one to slope, and another was related to distance along axis from the canyon head (Mortensen & Buhl-Mortensen 2005).

Broad scale studies of gorgonian biogeography in the North Atlantic (Watling & Auster 2005) found large provinces comparable to deep-water Scleractinia (Cairns & Chapman 2001). In the North Pacific, octocorals were broadly distributed relative to Scleractinia, with frequency peaks in different depth ranges for different families (Etnoyer & Morgan 2005). Data from these studies were incorporated in an Ecological Niche Factor Analysis to predict deep gorgonian habitat (Bryan & Metaxas 2007). The continental shelf break was identified as high quality habitat, but bathymetry was coarse (4 km resolution), so the model could not resolve known gorgonian habitat on the continental shelf (Etnoyer & Morgan 2008). Gorgonians grow large and abundant on intermittent, low relief substrate so high-resolution bathymetry and substrate maps are required to adequately resolve habitat.

Fundamental questions about deep-octocoral distribution must be addressed before predictive modeling efforts can be effective. This dissertation is limited to two independent variables, depth and location, to establish a framework, to minimize spurious associations, and to test Bayer's hypothesis of a cosmopolitan distribution in deep-water. The intention of the study is to improve management and conservation through better understanding of deep-water octocoral assemblages, and improved knowledge of octocoral diversity and distribution in the Gulf of Mexico.

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## CHAPTER ONE

### Distribution and Diversity of Octocorals in the Gulf of Mexico

by

Peter J. Etnoyer & Stephen D. Cairns

Running head: Gulf of Mexico octocorals

Key words: octocoral, deep-water, deep-sea, biogeography, distribution, Gulf of Mexico

## Distribution and Diversity of Octocorals in the Gulf of Mexico

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**ABSTRACT:** Octocorals are broadly distributed throughout the world's oceans, but few studies address the depth and distribution of octocoral genera at the basin scale. A meta-analysis of 1881 octocoral occurrences was conducted in the Gulf of Mexico to assess the distribution and diversity of octocorals by depth and by region. Records were assembled from cruise reports and museums. Analyses included univariate and multivariate tests supported by hierarchical clustering and multi-dimensional scaling techniques using Bray-Curtis similarity matrices. Significant differences in the composition of octocoral assemblages were evident between depth zones and regions, but there was no significant difference in diversity between depth zones deeper than 800 meters. Assemblage structure was evident as deep as 1600 m. Gorgonians were predominant. Shallow-waters (less than 50 m) were characterized by the Plexauridae and Gorgoniidae. Intermediate depths (50 - 800 m) were characterized predominantly by the Ellisellidae and Paramuriceidae. Deeper than 800 m, gorgonians in the Isididae, Chrysogorgiidae and Primnoidae were predominant. Diversity was highest in the Straits of Florida and northwest Gulf of Mexico. The Mexican (southern) Gulf was not well represented because of insufficient reporting and/or research effort. The hypothesis of two biogeographic regions within the Gulf was strongly supported by the analyses, with heterogeneity extending into the deep sea, contrary to previous assumptions.

## INTRODUCTION

Deep-water corals are increasingly recognized as important habitat formers in deep-sea environments, but our understanding of deep octocoral distribution within ocean basins is limited, because only a few basin scale analyses exist. The Gulf of Mexico is a good area for developing better understanding of octocoral distribution because research effort is high relative to most other large marine ecosystems. Biological surveys began in the Straits of Florida, 1867-1870, aboard the U.S. Coast Survey Steamer *Blake*, and continued aboard the U.S. Fish Commission *Albatross* into the mid-1880's (Giammona 1978). Octocorals from these expeditions were described in seminal taxonomic studies (Deichmann 1936, Bayer 1961). Bayer (1954) treated the Gulf of Mexico as a primary subject, a tradition that continues to this day. It is the only sea basin in the Western Hemisphere with a comprehensive octocoral inventory (Cairns & Bayer 2009a).

Octocorals (sea fans, sea pens, soft corals, gorgonians) are some of the most common and conspicuous sessile benthic megafauna in the Gulf of Mexico and Caribbean Sea (Cairns 1977), but they occur worldwide on hard and soft substrates (Bayer 1956, 1961) deeper than 5800 m (Cairns & Bayer 2009b). Their depth range and substrate preferences imply a broadly distributed habitat type. Gorgonians create structural complexity in a relatively featureless environment, generating substrate for fish (Heifetz 2002, Etnoyer & Warrenchuk 2007), invertebrates (Krieger & Wing 2002, Buhl-Mortensen & Mortensen 2005), and microbial fauna (Penn et al. 2006).

Habitat qualities are often attributed to the matrix-forming scleractinian *Lophelia pertusa*, but the depth range of *L. pertusa* is relatively small (200 – 1000 m, Schroeder et al. 2005) compared to octocorals. Some ocean basins appear to lack bioherms altogether,

whereas gorgonians grow large and abundant (Etnoyer & Morgan 2005), functionally replacing bioherm habitats. Thus, octocorals are important subjects of study, and recently, of federal legislation (Magnuson-Stevens Act, 16 U.S.C.A. 1853(b)(105)).

Species richness of deep-water scleractinian corals was mapped worldwide (Cairns 2007). The pattern of richness mirrored shallow (< 50 m) scleractinians (Veron 1995). No global study of octocorals is available. Basin scale investigations in the North Atlantic (Watling & Auster 2005) and the Northeast Pacific (Etnoyer & Morgan 2005) have proven useful for habitat modeling (Leverette & Metaxas 2007) and estimation of fisheries impacts (Morgan et al. 2005). Federal studies (Lumsden et al. 2007) provide the broadest, most comprehensive overview of deep coral distribution at a large scale.

The Gulf of Mexico is a good subject for a regionally comprehensive review of octocoral distribution and diversity with relatively high taxonomic resolution; because 185 species of octocorals are documented (Cairns & Bayer 2009b) and a biogeographic model is established. A shallow West Indian Province “invades from the south” comprised of *Eunicea*, *Muricea*, *Plexaurella*, and *Pseudopterogorgia* spp. (Bayer 1961). A Carolinian Province comprised of *Muricea pendula* and *Leptogorgia* spp. occurs along the northern coast (Bayer 1961, Briggs 1974). Deep-water octocoral habitat in the Gulf is characterized as regionally cosmopolitan, Paramuriceidae and Ellisellidae typical of the West Atlantic, ranging as far east as the Caribbean Antilles. Discharge from the Mississippi River is presumed not to affect deep-octocoral distribution (Bayer 1961). Three Gulf assemblages are supported by Gimmona (1978): a shallow West Indian assemblage, northwest Gulf banks assemblage, and a deep-water group, presumed to be homogeneous throughout the Gulf (Giammona 1978).

A meta-analysis of 1881 octocoral records from several different reports and institutions was used to characterize Gulf of Mexico octocoral habitat by depth and by region. Sample size has tripled in the thirty years since Giammona (1978) first subdivided the Gulf into 61 geographic subunits to compare family richness. In this study, lower taxa (genus or species) were used to investigate the patterns proposed by Bayer (1961) and Giammona (1978). We ask: Which octocoral genera and species are common, which are rare? Are there differences between depth zones and regions? Does diversity decrease with depth? Does homogeneity increase with depth? Finally, we ask: Where is the most diverse assemblage of octocorals in the Gulf of Mexico?

## **MATERIALS AND METHODS**

A total of 1881 unique octocoral records were gathered from five institutions and six reports (Giammona 1978, CSA & TAMU-GERG 2001, Cunningham 2002, Reed et al. 2005, 2006, Brooks et al. 2008). “Unique” is defined as a single occurrence of an octocoral species not shared by other institutions or reports. Museums contributed most (78 %) records, and these typically referenced voucher specimens. Contributors included the Smithsonian Institution National Museum of Natural History (NMNH), Texas Cooperative Wildlife Collection at Texas A&M University (TCWC), Museum of Comparative Zoology at Harvard University (MCZ), Harbor Branch Oceanographic Institute at Florida Atlantic University (HBOI), and Yale Peabody Museum at Yale University (YPM). YPM records were retrieved online through the Global Biodiversity Information Facility (GBIF, [www.gbif.net](http://www.gbif.net), 2009-04-28) (Table 1).

**Table 1. Contributing institutions and records available to the Gulf of Mexico octocoral database.** Giammona- Giammona (1978) ; HBOI- Harbor Branch Oceanographic Institute, including (Reed et al. 2005, 2006); MCZ – Museum of Comparative Zoology, Harvard University; MMS - Minerals Management Service, three projects (MMS 2000, Cunningham 2002, MMS 2008); NMNH – Smithsonian Institution National Museum of Natural History; TCWC – Texas Cooperative Wildlife Collection at Texas A&M University; YPM – Peabody Museum of Natural History, Yale University (Accessed through GBIF Data Portal, www.gbif.net, 2009-04-28). "Unique" records represent a single occurrence not shared by other institutions, with replicate samples deleted to standardize effort and collection methods. Rows with unique records comprise the database, as detailed in the last row.

	<b>Giammona</b>	<b>HBOI</b>	<b>MCZ</b>	<b>MMS</b>	<b>NMNH</b>	<b>TCWC</b>	<b>YPM</b>	<b>Total</b>
Records available	630	125	218	57	2086	230	17	3363
Records w/ depth	274	125	0	57	2006	229	0	2691
Unique w/ depth	154	35	0	57	1073	187	0	1506
Unique w/o depth	193	0	112	0	57	0	13	375
Database records	347	35	112	57	1130	187	13	<b>1881</b>

Records were reduced to common fields for institution, institutional identifier, latitude, longitude, depth in meters, order, family, genus, and species. Collection methods ranged from dredges to manned submersibles. Duplicate species records within 1 km of each other were removed to normalize effort, standardize reporting, and introduce statistical independence. Records without coordinates and duplicates shared by more than one institution or report were deleted to produce unique records. The unique records were imported to a Geographic Information System (GIS) ArcGIS 9.2 (ESRI 2008). Data were treated as random and independent to justify multivariate and univariate comparisons.

Taxonomic quality control was imposed following a recent inventory of Octocorallia in the Gulf of Mexico (Cairns & Bayer 2009b). Gorgonacea (sea fans and sea whips) was treated as distinct from Alcyonacea (soft corals). Paramuriceidae was treated as distinct from Plexauridae based on molecular evidence (Wirshing et al. 2005). All junior synonyms were subsumed to senior synonyms. All varieties were subsumed into species. Species names no longer in use were subsumed into current species. Suspect records and mis-identifications were deleted or subsumed into genus. Records higher than family (e.g., Gorgonacea) were deleted. Family and genus level records were excluded in

richness estimates, but they were included in the multivariate analysis because they help to establish the character of the zone in the Bray-Curtis similarity matrix.

Genus records could be interpreted as: 1) species not described, or 2) species not determined. When “Genus sp.” was known to represent an undescribed species, it was included (e.g., *Hypnogorgia* sp.). When Genus sp. represented an *unidentified* species (this is common) the record was excluded from richness and diversity exercises *unless no other representative of the genus was present*. For example, if specimens in 5 species in the genus *Thesea* (*T. rubra*, *T. nivea*, etc.) were listed with specimens labeled *Thesea* sp., *Thesea* sp. was deleted from the accumulation. If no species of *Thesea* were listed in the Gulf, only *Thesea* sp., the records were maintained. The assumption was that at least one species of *Thesea* was known to occur in the Gulf. It was unidentified, but still present. A total of 204 distinct taxonomic units (hereafter “species”) resulted from the taxonomic review, including 12 unidentified species in genera not otherwise represented.

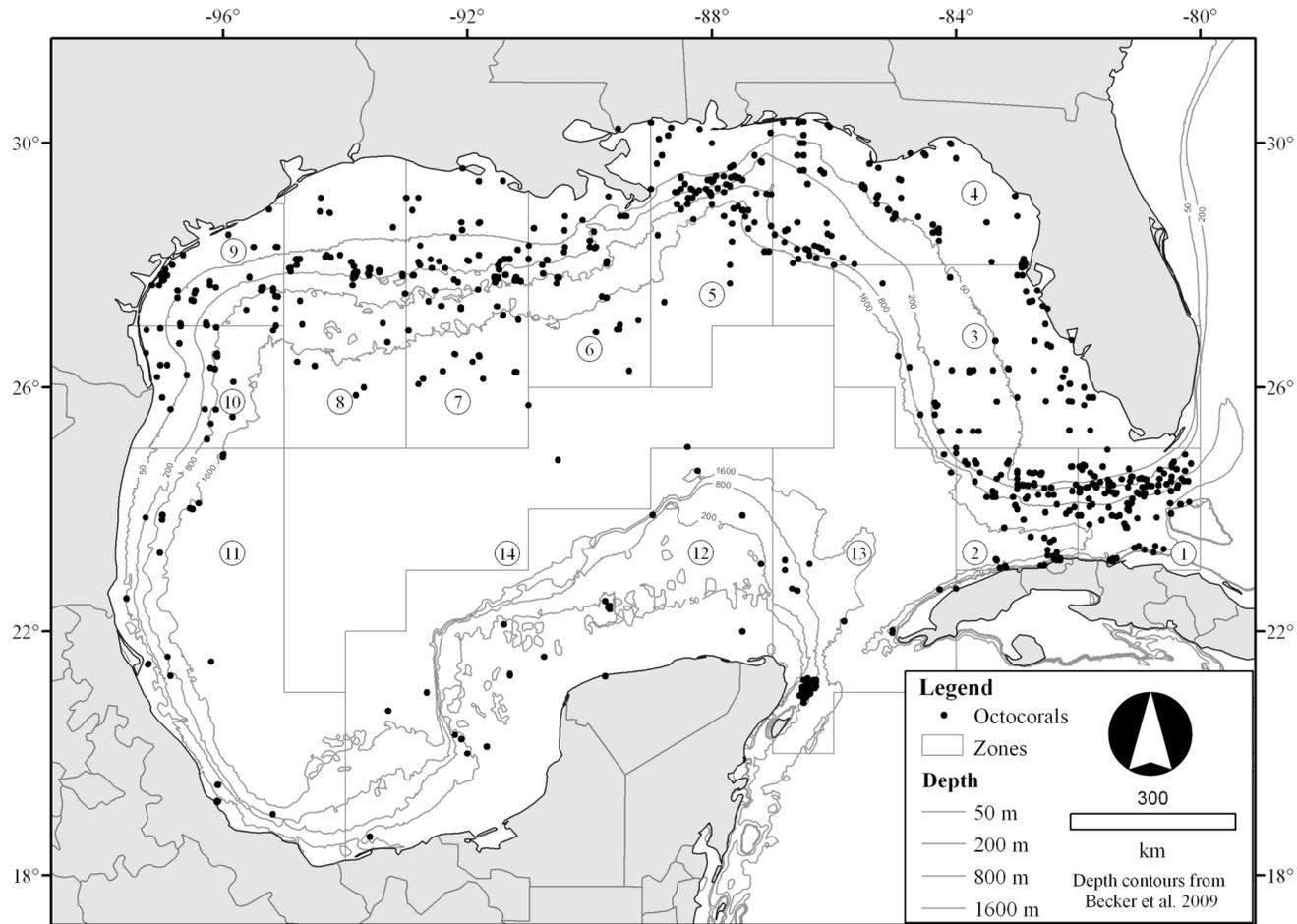
A subdivision scheme was imposed on the Gulf using the GIS to generate sample units for comparison. The scheme was an iteration of a method developed to study Gulf of Mexico shrimp populations (Kutkuhn 1962), later adapted to analysis of octocorals (Giammona 1978). The technique used lines of latitude and longitude to organize spatial data into sample units. The model was improved by intersecting a 2° ‘fishnet’ with isobaths in meters (m) derived from the best available bathymetry data, a blended product of satellite altimetry and coastal survey data (SRTM 30 – Becker et al. 2009).

Isobath values (0 m, 50 m, 200 m, 800 m, 1600 m) were derived from the depth distribution of the octocoral data using the natural breaks (Jenks) method in ArcGIS 9.2. Jenks is a variance-minimization classification scheme that groups similar values and

maximizes differences between classes (Slocum 1999). Values were rounded to reflect common nomenclature (e.g., > 50 m = deep water, > 200 m = deep sea). The result was 2° parallels bounded by isobaths on two sides. Polygons were merged to approximate balanced sample sizes. The result was 63 unequally sized sample units (Fig. 1), 13 zones subset into five depth classes: (1) 0 – 50, (2) 50 – 200, (3) 200 – 800, (4) 800 – 1600, and (5) 1600 m+. Two zones did not include depths greater than 1600 m. Zone 14 was abyssal, with only one data point (Fig. 1).

Zones 1 and 2 were referred to as the southern Straits of Florida, to distinguish the Gulf Straits from the West Atlantic Straits between Florida and the Bahamas. All zones were assigned directional factors to test for multivariate differences between regions. Zones 1-3 were defined as east, zone 4 was northeast, zones 5 - 8 were north, zone 9 was northwest, zone 10 – 11 were west, and zones 12-13 were south. Octocoral occurrences were assigned values for depth class and zone using “extract values to point feature” command in ArcGIS 9.2. Assigned values were cross-checked against reported depths.

Depth values for some records (~25 %) were misclassified because of coordinate position. These were corrected following this example. Consider a coordinate position close to a boundary, e.g., inside the 800 -1600 m upper boundary. The data point was classified as 800 – 1600 m, due to imprecise coordinates, but the reported depth was 750 m. In this case, the depth classification would be corrected to the 200 – 800 m depth range. When no depth was reported, the geographic classification was assumed to be correct. Resulting data were prevalence, not incidence, because sample units could have > 1 occurrence of a species.



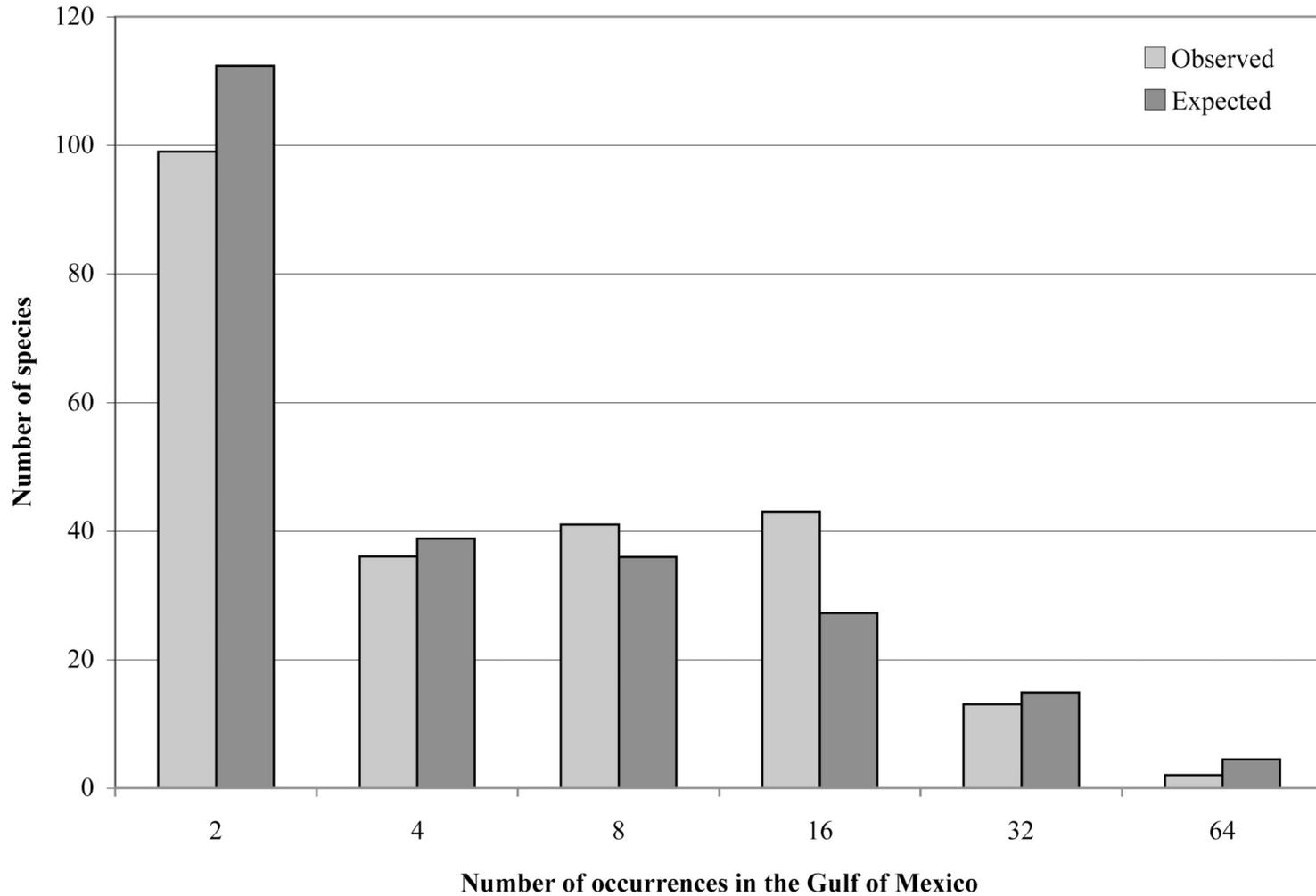
**Figure 1. Map of octocoral occurrences in the Gulf of Mexico.** Octocoral occurrences (1881, black dots) are superimposed on 14 numbered zones (polygons) of comparable sample size. The polygons are irregular, bounded by parallels of longitude and latitude, and subdivided by bathymetric isobaths from SRTM30 bathymetry (Becker et al. 2009) of 5 depths zones (0-50 m, 50-200 m, 200-800 m, 800-1600 m and 1600 + m) resulting in 63 functional subunits. Zone 14 was not analyzed. Zones 1 and 9 do not exceed 1600 m.

The frequency distribution of species would approximate, but not achieve, a log series distribution (Kolmogorov-Smirnov,  $df = 4$ ,  $p > 0.05$ ) (Fig. 2). Therefore, the non-parametric, sample-based richness estimator Chao 1 was used to generate randomized species accumulation curves in EstimateS 8.0 software (Colwell 2006). Chao I yields a minimum estimate (Magurran 2004). The technique maintains the relationship between richness and individuals to preserve heterogeneity in comparisons of regional species richness. Chao 1 also provides an estimate of asymptotic richness, and some measure of completeness of surveys (Levin et al. 2001).

Species accrual curves were plotted by depth zone, and for all depths by pooling zones together. Chao 1 is inappropriate across large ecological gradients (Magurran 2004), so Simpson's  $\lambda$  was used in the form  $(1 - \lambda)$  to compare diversity between depth zones and sample units. Species richness, Fisher's  $\alpha$ , and Shannon-Wiener index were also considered. Simpson's is non-parametric, robust to variation in sample size, and weights abundant species highly. This was desirable because abundant species should be the most consistently and correctly identified (Carney 2007).

To test for significant differences in diversity between depth zones, Simpson's index was averaged across regions ( $< 1600$  m,  $n = 13$ ;  $> 1600$  m,  $n = 9$ ). The non-parametric Kruskal-Wallis test was paired with a modified Scheffe's post-hoc test to identify pairwise differences between unequal sample sizes ( $df = 4$ ,  $p = 0.05$ ). Scheffe's test is parametric, not an ideal fit, but was justified in this case because the univariate test is highly conservative, with small chance of Type I error (Day & Quinn 1989).

Multivariate techniques consisted of hierarchical cluster analyses and non-metric multi-dimensional scaling (MDS) ordinations based on Bray-Curtis similarity matrices



**Figure 2. Frequency of occurrence for octocoral species.** Frequency distribution for 204 species in 1881 occurrences (black bars) with expected log series distribution (white bars). The frequency distribution approximates, but does not conform to a log series distribution (Kolmogorov- Smirnov,  $df = 4$ ,  $p > 0.05$ ).

calculated using PRIMER 6.1 software (Clarke & Gorley 2006). No data transformation was applied. The analysis of similarity (ANOSIM) Global R statistic was used to identify significant differences between depth zones and regions at level  $p = 0.05$ . A SIMPER test (similarity/distance percentages) was used to determine the contributions of each variable to the average similarity within a group for comparisons between regions (Clarke 1993). The similarity profile (SIMPROF) procedure was employed to test for structure in the data within depth zones. Bubble plots were employed to describe the species and genera responsible for separation between groups (Field et al. 1982).

The data are a collection of historical records; most samples were collected in the last 50 years, but some records date back to the 19<sup>th</sup> century (Heilprin 1890). Changes in climate and sediment, burial and exhumation processes from hurricanes, and natural life cycles of octocorals imply that some colonies may no longer exist where they were collected. Deep-sea gorgonian lifespans can exceed decades (Andrews 2005). Ages of shallow and intermediate gorgonians are undetermined. Gorgonian assemblages are probably not ephemeral, but hurricanes are frequent, and benthic impacts from these storms may result in colony burial or overturning.

Furthermore, octocoral data were not originally collected for the purpose of our hypothesis testing, so no sampling design was imposed upon the original collections. Our approach made fundamental assumptions of random, independent data to justify the comparisons, thus the results must be viewed with some caution. The costs of a directed field study of this magnitude would be insurmountable, so this retrospective analysis was put forward as the best possible effort to realize the distribution of deep-sea corals using available data. Every effort was made to standardize disparate data sets in order to

produce an accurate representation of octocoral depth, distribution, and diversity in the Gulf of Mexico at the highest possible taxonomic resolution.

## RESULTS

We collected a total of 1881 octocoral records in the Gulf of Mexico from 204 species in 92 genera in the orders Alcyonacea, Gorgonacea, Helioporacea, and Pennatulacea. Gorgonacea were the most commonly collected, with 1581 records from 65 genera and 160 species. Six species were unidentified from the genera *Acanthacis*, *Anthomuricea*, *Hypnogorgia*, *Metallogorgia*, *Paragorgia*, and *Radicipes*. Alcyonacea were the second most commonly collected, with 178 records from 15 genera and 25 species. One species was unidentified, from the genus *Clavularia*. Pennatulacea were third most commonly collected octocoral, with 121 records from 19 species in 13 genera. Five specimens were unidentified species in the genera *Balticina*, *Kolphobelemnon*, *Sclerobelemnon*, *Scleroptilum*, and *Scytalium*. Helioporacea was comprised of a single occurrence of the species *Epiphaxum breve*.

The most commonly collected octocorals in each of the three major Orders were mesophotic (typically > 50 m) and deep-sea (typically > 200 m) organisms (Table 2). Deep-sea *Acanella* sp. (bamboo coral) was the most commonly collected gorgonian genus, with reported depths ranging from 265 - 2857 m. *Thesea* sp. was the second most common genus, with a reported range from 25 – 380 m. Only one record was < 50 m. The midwater gorgonian *Scleracis guadalupensis*, and deep-sea gorgonians *Acanella eburnea* and *Chrysogorgia elegans* were the most commonly collected octocoral species. The most commonly collected Alcyonacea were all from mesophotic depths, except for

**Table 2. Octocorals most commonly collected in the Gulf of Mexico.** The most commonly collected octocorals in the Gulf of Mexico by taxa and by frequency, from 1847 genus-level and 1395 species-level occurrences. A cross [†] indicates shallow octocorals (< 50 meters), an asterisk [\*] indicates deep octocorals (> 200 m), and a dash [-] indicates mesophotic octocorals (50 - 200 m).

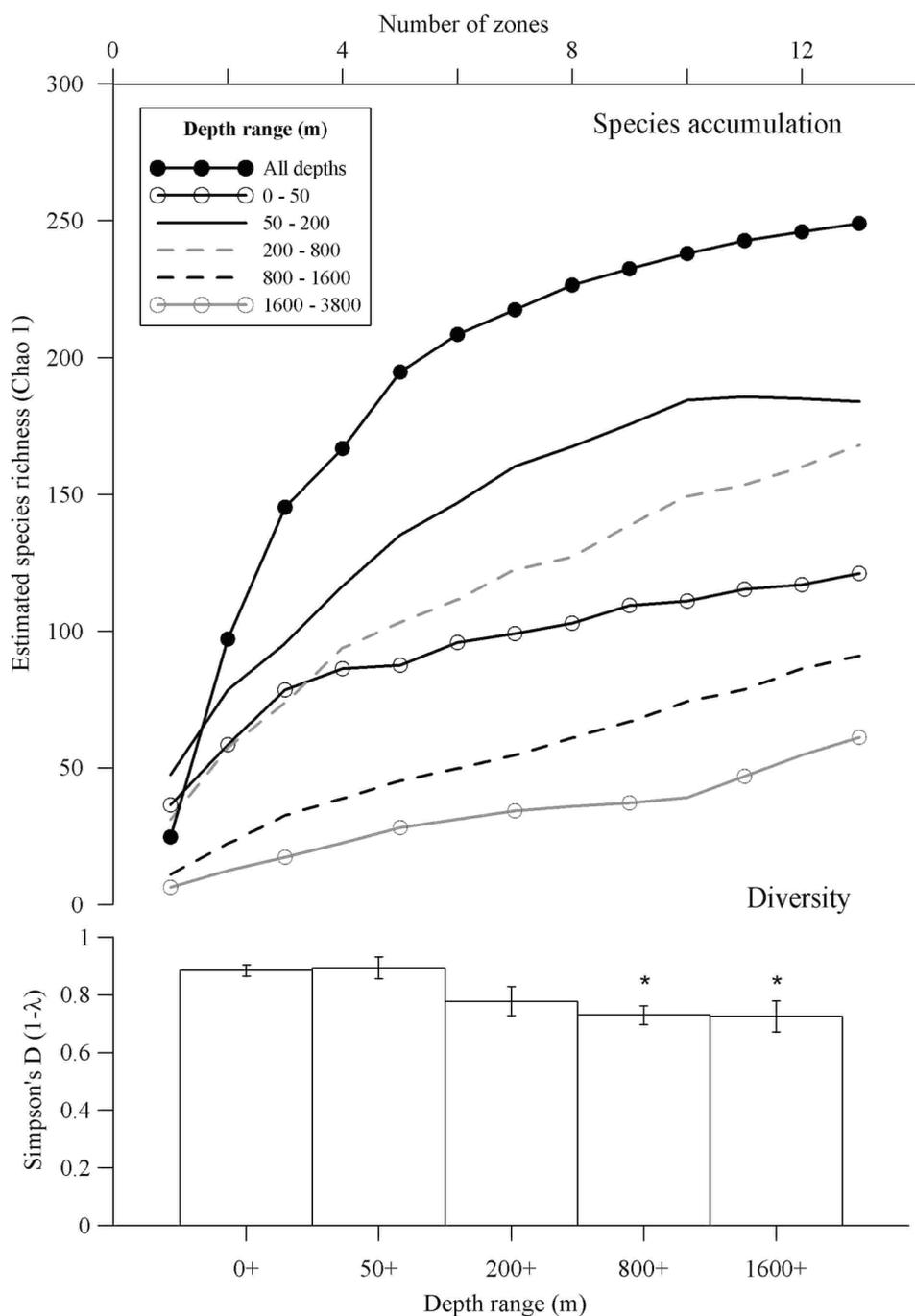
ALCYONACEA		Frequency	Depth
<b>Genus</b> n = 177	<i>Telesto</i>	0.0352	-
	<i>Nidalia</i>	0.0120	-
	<i>Siphonogorgia</i>	0.0120	-
	<i>Sarcodictyon</i>	0.0080	-
<b>Species</b> n = 181	<i>Telesto sanguinea</i>	0.0144	-
	<i>Nidalia occidentalis</i>	0.0130	-
	<i>Siphonogorgia agassizii</i>	0.0101	-
	<i>Telesto flavula</i>	0.0072	-
	<i>Telesto riisei</i>	0.0065	†/ -
GORGONACEA			
<b>Genus</b> n = 1551	<i>Acanella</i>	0.062	*
	<i>Thesea</i>	0.061	-
	<i>Leptogorgia</i>	0.053	†
	<i>Nicella</i>	0.045	-
	<i>Ellisella</i>	0.044	-
<b>Species</b> n = 1136	<i>Scleraxis guadalupensis</i>	0.0245	-
	<i>Acanella eburnea</i>	0.0238	*
	<i>Chrysogorgia elegans</i>	0.0224	*
	<i>Leptogorgia virgulata</i>	0.0188	†
	<i>Pseudopterogorgia acerosa</i>	0.0181	†
PENNATULACEA			
<b>Genus</b> n = 119	<i>Funiculina</i>	0.0120	*
	<i>Umbellula</i>	0.0110	*
	<i>Renilla</i>	0.0100	†
<b>Species</b> n = 78	<i>Funiculina quadrangularis</i>	0.0159	*
	<i>Renilla muelleri</i>	0.0123	†
	<i>Virgularia presbytes</i>	0.0065	†/ -

one species, *Telesto riisei*, which can occur in shallow water. Pennatulaceans were predominantly represented by the sea pen *Funiculina quadrangularis*, the deepest of all octocorals, with a remarkable range from 55 – 3075 m (Fig. 3).

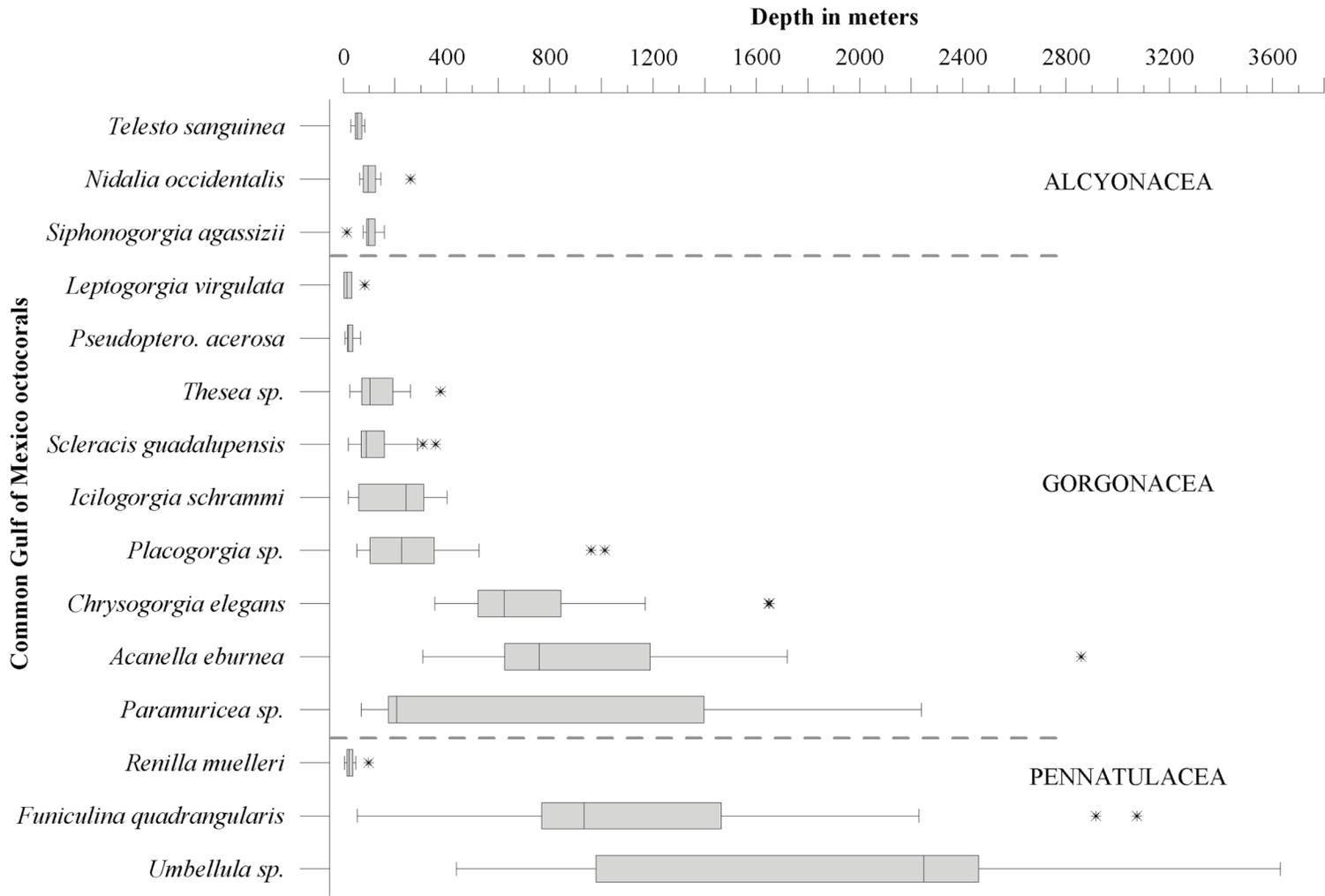
Shallow water species were among the most commonly collected in all three Orders, but they did not rank highest (Table 2). *Leptogorgia virgulata* ranked fourth among Gorgonacea. All but one of the depth records were < 33 m. The sea plume *Pseudopterogorgia acerosa* is a familiar component of West Atlantic reefs, and also common in the Gulf of Mexico. It was fifth among the top five most common species, with a reported range from 7 – 40 m, and one record at 68 m. Shallow alcyonacean soft corals were represented by *Telesto riisea*. The sea pen *Renilla muelleri* was more commonly collected than most soft corals. *Virgularia presbytes* was collected nearly as often as the soft coral *T. riisea*.

No single species comprised > 4% of the total number of samples. The two most commonly collected genera, *Acanella* and *Thesea*, together comprised 11.3% of the total samples. Of the remaining species, > 1/3 were rarely collected, 25% of species occurred only once, and 13 % occurred twice. Among the rarely collected species were species from common genera (*Nicella americana*, *Callogorgia linguimaris*), and common shallow water species (*Gorgonia flabellum*, *Pseudopterogorgia bipinnata*). Some genera that occurred rarely among the samples were common in other ocean basins (*Paragorgia* sp. in North Atlantic, *Corallium* sp. in Hawaii).

Sample based species accumulation curves using the non-parametric Chao 1 estimator predicted 250 octocoral species (Fig. 4) in the Gulf of Mexico. The 95% confidence intervals surrounding the expected richness estimate ranged from 228 to 293



**Figure 3. Species accumulation and average diversity by depth.** (A) Species accrual by depth, and for all depths pooled (black line, solid circles), using the non-parametric Chao I sample based species richness estimator. (B) Diversity (Simpson's  $D$ , form  $1 - \lambda$ ) for each depth range, averaged across all zones with standard error. Asterisks indicate depth ranges with significantly lower diversity (Kruskal-Wallis,  $df = 4$ ,  $p < 0.05$ ).



**Figure 4. Depth range for the most common octocorals in three orders.** Boxplots with depth ranges for the most commonly occurring octocorals in the groups Alcyonacea, Gorgonacea, and Pennatulacea from the Gulf of Mexico. Minimum, lower quartile, median, upper quartile, and maximum values are depicted in boxplots. Asterisks indicate outliers.

species. The rate of species accrual for all zones pooled was highest for mid-depths (50 – 200 m) and deep-sea (200 – 800 m), but confidence intervals overlapped. Lowest rates of accrual were from the deepest zones (800 – 1600 m, 1600 m +).

The average Simpson's diversity indices of samples from mid-water depths were not significantly different than the average Simpson's diversity indices of samples from shallow-water (Kruskal-Wallis adjusted H,  $df = 2$ ,  $p > 0.05$ ; Table 3; Fig. 3). However, average Simpson's diversity index of samples from the deepest zones (800 – 1600, 1600 m +) was significantly lower (Scheffe's test,  $p < 0.05$ , Appendix 1) than the diversity index of the samples from shallow, mesophotic, and deep-sea zones. That is, no significant loss of octocoral diversity was evident in samples shallower than 800 m.

Significant differences in species composition were found between samples from different depths (MDS; ANOSIM Global R,  $df = 4$ ,  $p < 0.05$ ) and regions (ANOSIM Global R,  $df = 3$ ,  $p < 0.05$ ). No data transformation was necessary to achieve significance. Stress was moderate ( $> 0.10$ ) in the two dimensional graphic representation of the ordination, so more dimensions would be necessary to accurately depict the differences between groups. However, clear separation between shallow, mid-water, and deep-sea groups was evident in the two-dimensional ordination plot (Fig. 5). The deep-sea zones ( $> 200$  m) are clustered in the lower right corner of the diagram, while shallow water groups are clustered in the lower center and lower left, and mid-water zones are clustered in the upper center of the MDS plot.

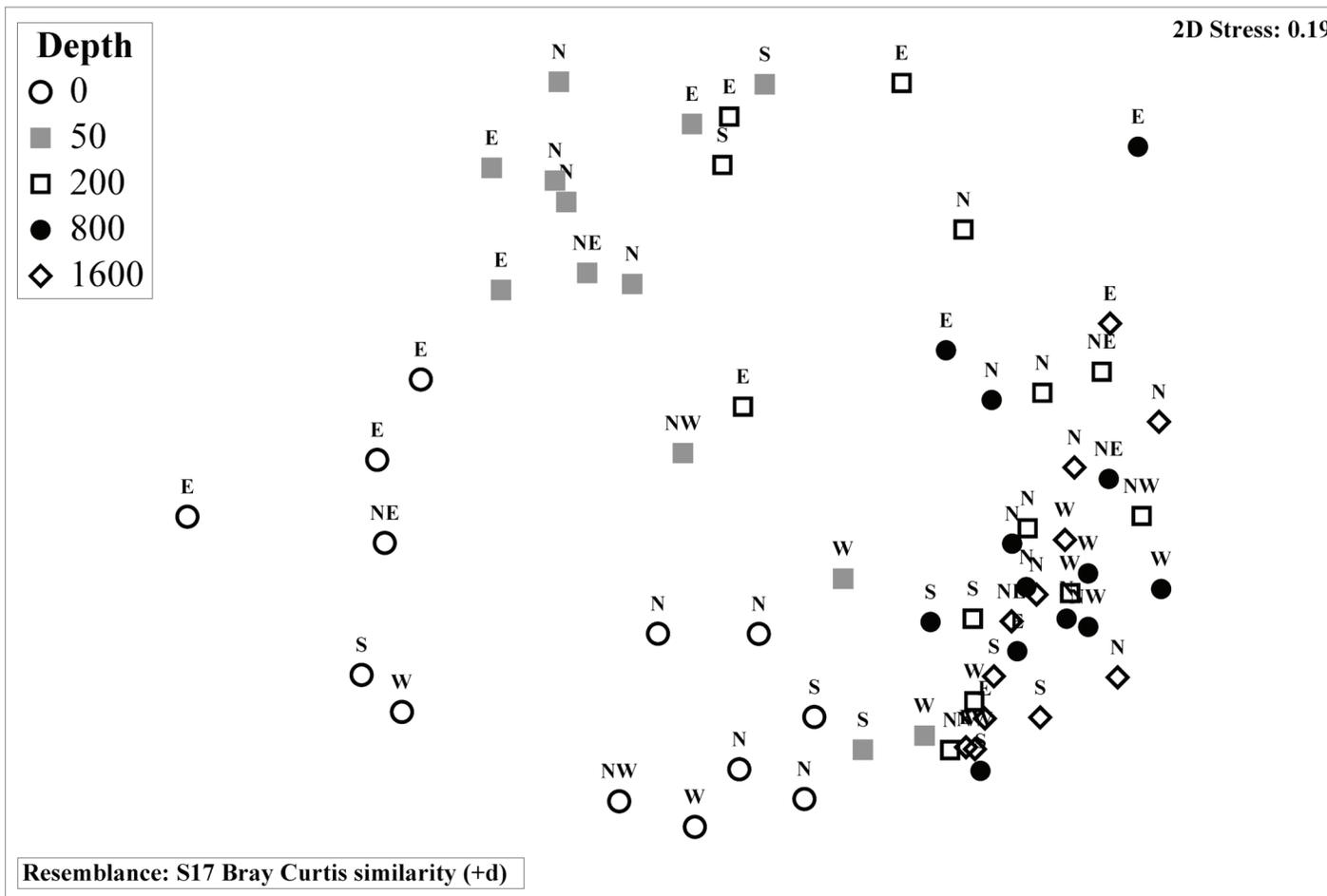
The northeast zone south of the Florida panhandle (zone 4, Fig. 1) was more similar to eastern zones (zones 1 – 3) than to northern zones (zones 5 – 8). The northwest zone (zone 9) was more similar to northern zones than to western zones (zones 10 – 11).

**Table 3. Top 10 ranks for octocoral diversity.** Sample units are labeled "Zone\_Depth", using zones in Figure 1, and depth as follows: 0 = 0-50 meters, 50 = 50-200 m, etc.. Zones discussed in the text are symbolized using *italics* for southern Straits of Florida, and **bold** for northern Gulf of Mexico. Simpson's index was the metric used to map octocoral diversity in Figure 8.

Rank	Simpson's D	Shannon's H'	Fisher's $\alpha$	Richness S
1	<i>2_0</i>	<i>2_0</i>	<i>2_0</i>	<i>2_50</i>
2	<i>2_50</i>	<i>2_50</i>	<i>2_1600</i>	<i>2_0</i>
3	<b>8_50</b>	<b>8_50</b>	<i>2_50</i>	<i>2_200</i>
4	<i>2_200</i>	<i>2_200</i>	<b>6_50</b>	<b>8_50</b>
5	<i>3_50</i>	13_200	<b>8_50</b>	<i>1_200</i>
6	13_200	<i>3_50</i>	<i>3_200</i>	13_200
7	<i>1_200</i>	<i>1_200</i>	<i>2_200</i>	<i>3_0</i>
8	<i>3_0</i>	<i>3_0</i>	13_200	<i>3_50</i>
9	<b>7_50</b>	<b>7_50</b>	<i>1_200</i>	<b>5_50</b>
10	<i>1_0</i>	<b>5_50</b>	<b>5_0</b>	<b>7_50</b>

Based on this, zone 4 was subsumed into north and zone 9 was subsumed into east for the hierarchical cluster analyses. The greatest difference between regional samples was between samples from the northern region and samples from the eastern region. Records from the Yucatan Channel zone 13 (south) were most similar to records from the nearby Straits of Florida (east). Western and southern zones were poorly represented in the database and not well replicated, so differences between samples from these regions and others were largely undetected by these techniques.

Some degree of separation was evident within depth zones. Differences within shallow-water zones were most significant. Samples from shallow zones in the east and north were highly significantly different (ANOSIM Global R,  $p < 0.01$ ). Samples from shallow zones in the north and south were significantly different (ANOSIM Global R,  $p < 0.05$ ). Shallow samples from the east, northeast, and south clustered together in the MDS plot (Fig. 5). They are aligned to the left of the MDS plot, more distant from the "core" deep-sea zones than shallow water samples from the north, northwest, and west.

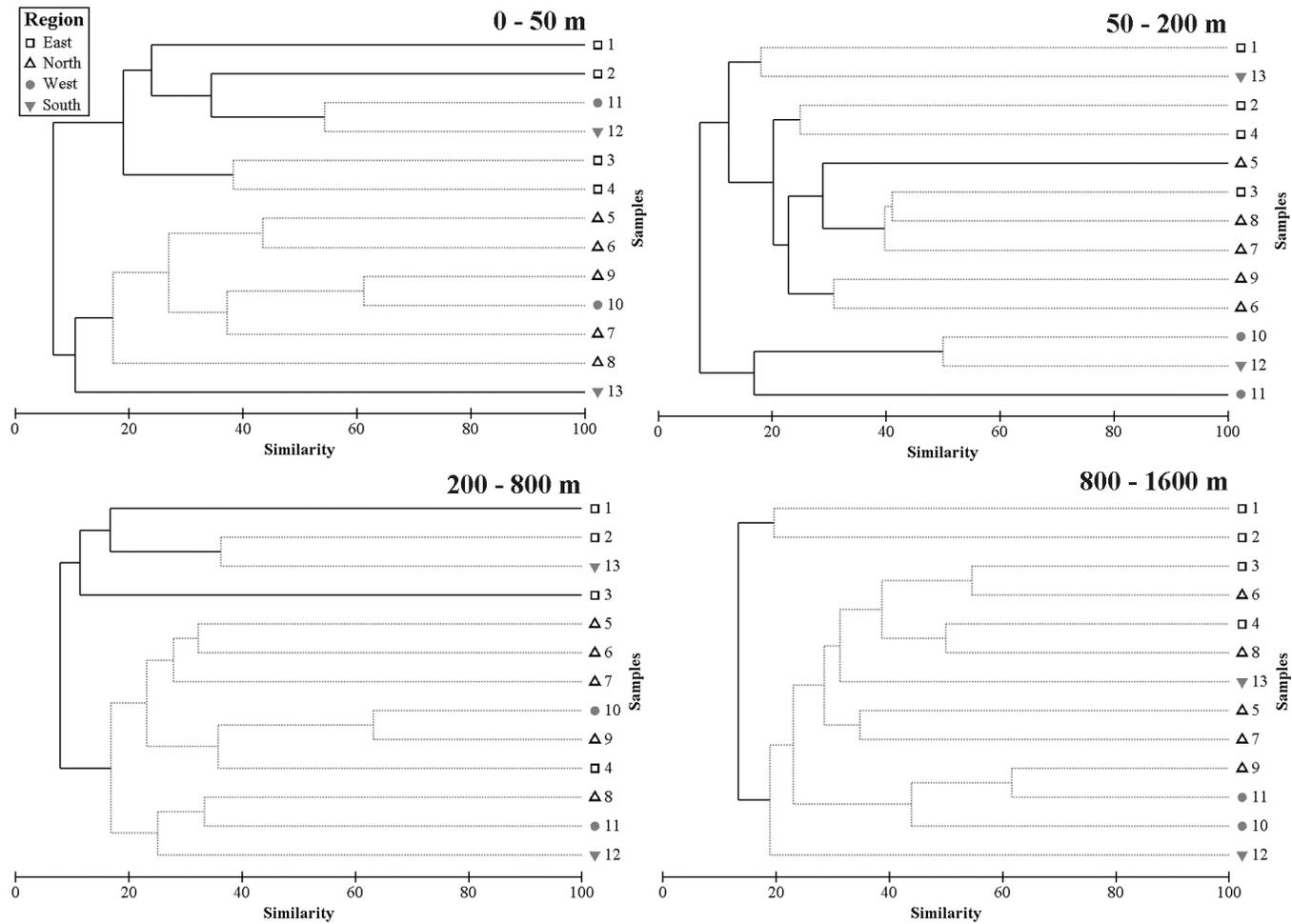


**Figure 5. A non-metric multi-dimensional scaling plot of sample units.** A non-metric multi-dimensional scaling (MDS) plot of 63 sample units in the Gulf of Mexico symbolized by depth (0 = Zero to 50, 50 to 200, and so on) and by region. The underlying similarity matrix is Bray-Curtis distance, based on the abundance of 200+ octocoral species. Deep-sea subunits (> 200 m) cluster together in the lower right. They were significantly different than shallow subunits (in the mid to lower left) (ANOSIM Global R,  $df = 5$ ,  $p < 0.01$ ) and mid-water subunits (in the middle top) (ANOSIM Global R,  $df = 5$ ,  $p < 0.05$ ).

Shallow water octocoral collections from Southern Florida, Cuba, the West Florida shelf, and the Florida panhandle were characterized by high richness and abundance, predominantly Plexauridae and Gorgoniidae. Low diversity and abundance characterized shallow-water octocoral collections on the continental shelf off Mississippi, Louisiana, and Texas; predominantly gorgonian species in the genera *Leptogorgia* and *Telesto*, and the sea pens *Renilla muelleri* and *Virgularia* sp. (listed in terms of relative abundance). A faunal transition between eastern zones and northern zones was evident in terms of decreased diversity and abundance west of Florida, as samples of Gorgoniidae and Plexauridae became increasingly absent.

Samples from the mid-water zones (50 – 200 m) in the north were significantly different from all others (ANOSIM Global R,  $p < 0.05$ ), but differences between the northern and eastern region were most pronounced. Paramuriceidae and Ellisellidae were typical in both regions. Mid-water collections in the eastern region were characterized by moderate abundance and high richness, predominantly *Thesea* sp., *Nidalia occidentalis*, *Telesto sanguinea*, and *Placogorgia mirabilis*. Mid-depth collections in the northern region were characterized by moderate to high abundance, high evenness, and high richness, predominantly *Nicella* spp., *Bebryce cinerea*, *Scleracis guadalupensis* and *Thesea* sp. Depressed abundance of samples and less than average richness were evident in zone 6, directly adjacent to the Mississippi Canyon.

Descending through the water column, there was a general trend of decreasing significance between regions. That is, the number of significantly different pairs was fewer, and the level of significance for the ANOSIM Global R statistic decreased. The pattern was illustrated by dendrograms with results of the SIMPROF procedure (Fig. 6).



**Figure 6. Hierarchical cluster dendrograms by depth.** A group average sorting strategy is applied to a Bray-Curtis similarity matrix of octocoral species abundance values. Zones are indicated on the vertical axis, symbolized by region. Similarity is shown on the horizontal axis. Solid black bars indicate significant differences (SIMPROF,  $df = 12$ ,  $p < 0.05$ ) between sample assemblages. Light gray bars indicate no significant difference.

SIMPROF tests for structure in the data: thick black bars in the cluster dendrogram illustrate significant differences between groups, and light grey bars illustrate non-significant differences between pairs. Differences between zones (structure in the data) were evident to a depth of 1600 m (SIMPROF,  $p < 0.05$ ). The number of groups decreased from 7 groups in the shallowest zones to four groups in the deep-sea, and two groups from 800 – 1600 m (Fig. 6).

Samples from the deep-sea zones (200 – 800 m) in the north and east were significantly different (ANOSIM Global R,  $p < 0.05$ ). Some substructure occurred within the eastern “bloc”. The west Florida shelf (zone 3) grouped separately from the eastern part of the Straits (zone 1) (Fig. 6). The deep Yucatan Channel (zone 13) was closely aligned with the deep western Straits (zone 2); these directly adjacent zones might be expected to be similar.

Samples from deep-sea zones in the eastern region had high average abundance and richness, predominantly *Chrysogorgia* spp., isidids *Keratoisis flexibilis* and *Acanella eburnea*, *Scleracis guadalupensis*, *Stereonephthya* and the primnoids *Plumarella pourtalesii* and *Callogorgia americana*. Samples from deep-sea zones in the northern region had lower abundance and richness, predominantly *C. americana*, *Muriceides hirta*, *K. flexibilis*, *A. eburnea*, and *Chrysogorgia spiculosa*. Abundance and diversity of samples were very low adjacent to the Mississippi Canyon, in zone 6 where 3 records of *C. a. delta* occurred, and in zone 8 where *Anthothela tropicalis* occurred only once, seaward of a mid-water zone of exceptional diversity. Sea pens *Funiculina quadrangularis* and *Protoptilum carpenterii* occurred in zone 9.

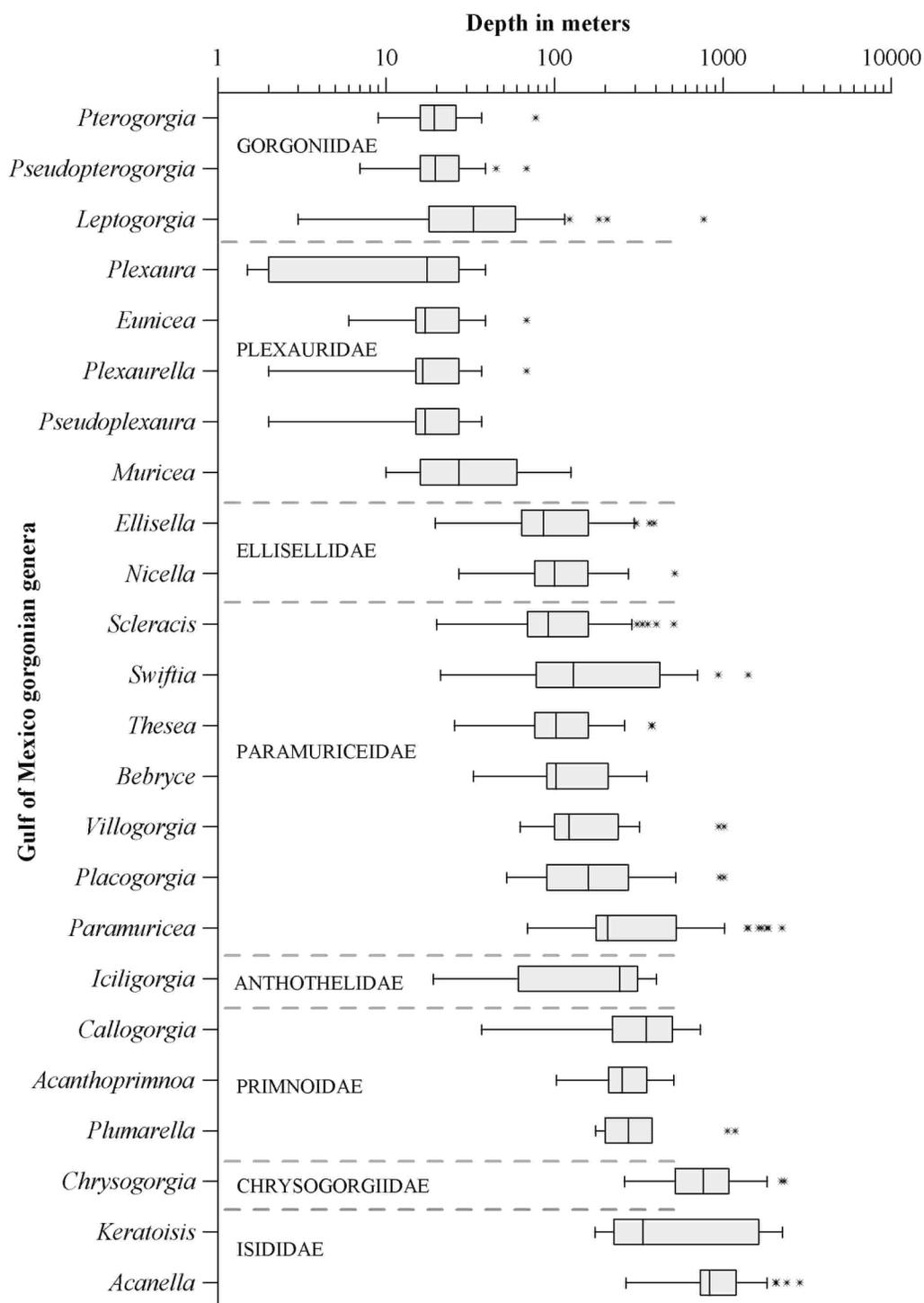
The sample assemblage from 800 – 1600 m depth in the eastern Gulf of Mexico was significantly different than the sample assemblage from 800-1600 m depth in the northern Gulf of Mexico (ANOSIM Global R,  $P < 0.05$ ). Average richness and abundance was higher in the east, attributable mostly to the exceptional character of the assemblage in the southern Straits of Florida. Primnoids *Narella pauciflora* and *Candidella imbricata* were abundant in the Straits. *Acanella eburnea* and *Chrysogorgia* spp. were typical of all zones. *Protoptilum* spp. and *Funiculina quadrangularis* sea pens occurred in low abundance in the Northern Gulf. Rare occurrences of *Chrysogorgia fewkesii*, *Iridogorgia pourtalesii*, and *Corallium medea* were documented west of Mississippi Canyon, in zone 7, by researchers using the DSV Alvin submersible (Brooks et al. 2008). Without these three records, data entries for the region would have been *A. eburnea* and *Chrysogorgia* spp., evidence that research effort is low at this depth, so the interpretation should be moderated.

There was no significant difference between regions deeper than 1600 m, partly due to the paucity of records. The western Straits (zone 2) was a notable exception, with low abundance, but fairly high generic richness for Gorgonacea, including *Paragorgia*, *Candidella*, *Narella*, *Paramuricea*, *Muriceides*, *Acanella*, *Chrysogorgia*, and *Metallogorgia*. The deep-sea pen *Umbellula* sp. was also present. Samples from the northern regions > 1600 m were characterized by few *Acanella eburnea*, *A. arbuscula*, *Iridogorgia pourtalesii*, *Keratoisis* sp. and *Paramuricea* sp. gorgonians, as well as the sea pens *Funiculina quadrangularis*, *Umbellula* sp., and *Acanthoptilum grandiflora*. Genus level identifications were more common at these depths than they were in shallower parts of the Gulf, presumably because the deepest species were poorly known.

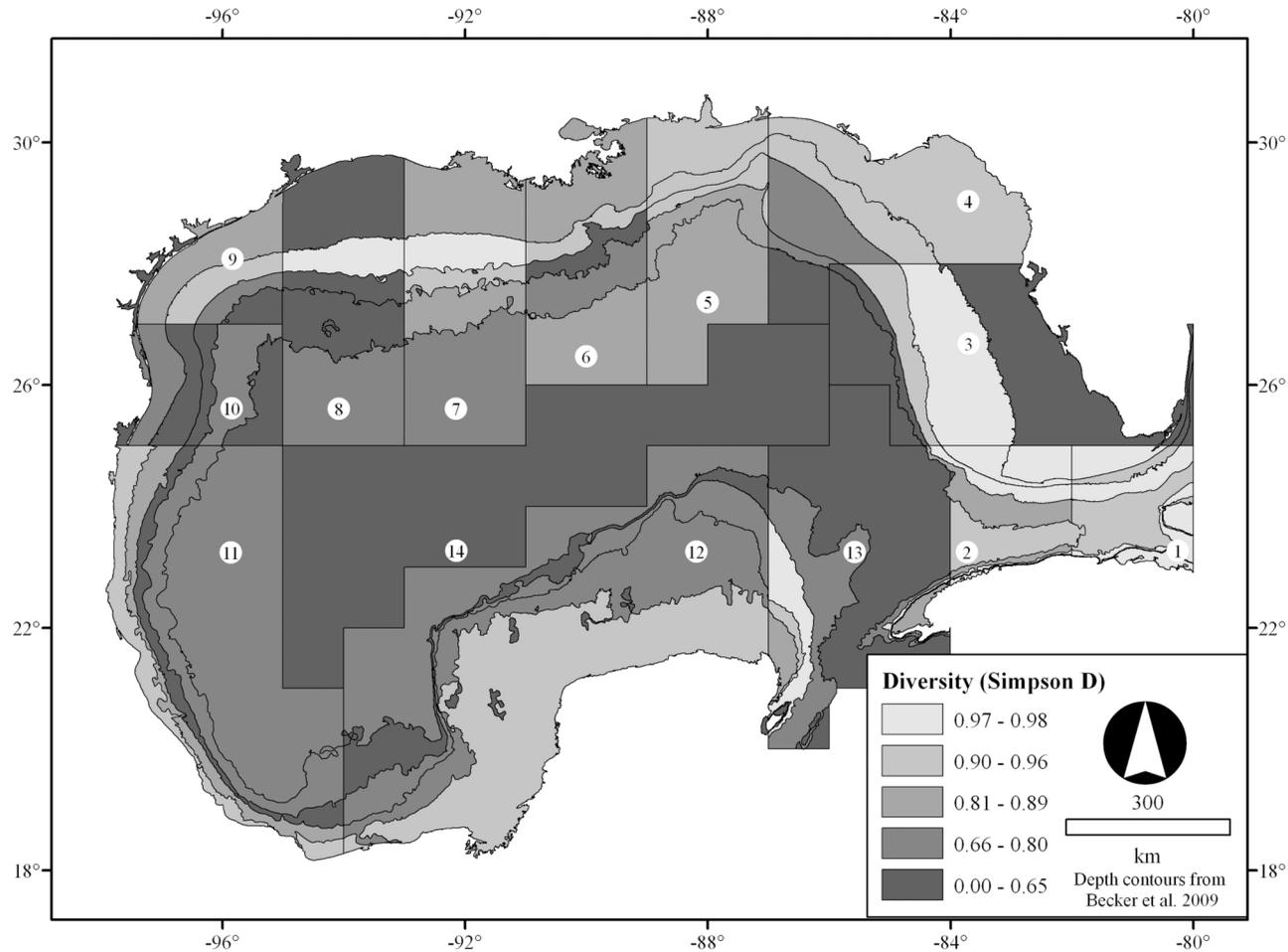
Given the large number of gorgonian samples available to this study, it seemed useful to plot the depth distribution of gorgonian genera to illustrate changes in the composition of the gorgonian assemblage with depth. To our knowledge, this has not been done for a broad spectrum of octocoral genera across their entire depth range. In the past, depth ranges were typically reported with maximum and minimum values. Good sample sizes ( $n > 12$ ) were available for 24 genera in 8 families, allowing for calculations of mean and standard error. The result was a fairly clear picture of faunal change with depth in log scale (Fig. 7). Bathymetric ranges of Plexauridae and Gorgoniidae were small, 1 – 50 m. Ellisellidae, Paramuriceidae, and Anthothelidae had intermediate ranges of 50 – 800 m, whereas the Chrysogorgiidae, Isididae, and some Primnoidae had large ranges, reaching from 250 m to the abyss.

A map was developed to illustrate octocoral diversity by depth and by zone. The diversity metric employed was Simpson's index, in the form  $1 - \lambda$ , where  $\lambda$  is the chance of selecting the same species twice. Where the chance was low, the diversity index was high. Two regions of high diversity are depicted in Figure 8. The high diversity area in the Straits was broad and deep, reaching to 800 m. Richness was highest in zones 1 and 2 in shallow and deep water. Zone 2 ranked first, second, and fourth for shallow-water (0 – 50 m), deep-water (50 - 200 m), and deep-sea octocoral diversity (200-800 m), respectively (Table 3).

In the northwest Gulf of Mexico, the high diversity zone was more depth restricted/dependent, on the outer continental shelf 100 km due west of the Mississippi Canyon in the Flower Garden Banks region. Zones 8 and 7 ranked third and ninth,



**Figure 7. Depth ranges of gorgonian genera in the Gulf of Mexico.** Depth ranges (in log scale) are shown for all gorgonian genera with suitable sample size ( $n > 12$ ). Minimum, lower quartile, median, upper quartile, and maximum values are indicated by boxplots. Asterisks show outliers. Genera are arranged by family, from shallowest to deepest.



**Figure 8. Map of octocoral diversity in the Gulf of Mexico.** Subunits from Figure 1 are color-coded to represent different levels of diversity (Simpson's  $D$ , form  $1 - \lambda$ ). The lightest shade shows the top 10 most diverse zones. Low diversity values (dark gray) indicate high probability of selecting the same species at random twice from any given subunit. The southern Gulf and abyssal seafloor were not well as well represented as regions in the north and east, but Simpson's index integrates effort through enumeration of evenness.

respectively, for deep-water octocoral diversity (50 – 200 m). Shannon-Weiner ranks of the top 10 were almost identical, and rankings by species richness had high concordance.

A linear regression of species to area based on well-sampled polygons (zones- 1 - 10) revealed no significant relationship ( $p > 0.05$ ). The correlation was slightly negative (-0.047). Highest richness was in small planimetric areas, partly a reflection of high vertical slopes. Southern Gulf polygons were large and under-sampled, so they were not included. No linear regression was performed comparing abundance and slope, or richness and slope because bathymetry was coarse (~1 km). A useful correlation may be accomplished using better resolution data (100 m) in the near future.

To summarize the results in the context of our research questions, deep-sea (*Acanella* sp.) and mesophotic (*Thesea* sp., *Scleraxis guadalupensis*) octocorals were most commonly collected, and about one third of octocorals species were rare. There were significant differences in species composition of samples between depths and between regions, but no significant difference in average diversity of sample units < 800 m. Differences between depths were reflections of changes in the species assemblage. Differences between regions reflected abundance and diversity, as well as species composition. There was evidence of structure in the data to 1600 m depth, but structure decreased with depth, supporting the hypothesis of increased homogeneity with depth. The highest octocoral diversity in the Gulf of Mexico was in the southern Straits of Florida and the northwest Gulf of Mexico.

## DISCUSSION

Enumeration of predicted species richness in the Gulf of Mexico was not a primary goal of this paper, but species accumulation curves were a by-product of our methods. The Chao 1 estimator predicted between 228 and 293 species in the Gulf, with a mean of 250 species. The actual number of species documented in the study was 204. Both richness estimates were considerably higher than a recent inventory (185 species - Cairns & Bayer 2009), a testament to the taxonomic completeness of the database that is not equaled, unfortunately, by the breadth of the spatial coverage.

Though coverage appears to be good, large parts of the Gulf remain to be explored, evidenced by sparse records in many zones, particularly the southern regions of the Gulf. We speculate that the old adage applies - absence of evidence is not evidence of absence. The broad vertical range of octocorals in the Gulf of Mexico (Figs. 3 and 7) would suggest that representatives of the subclass could be found at almost any depth less than 3400 m in the Gulf of Mexico. Sea-pens and some gorgonians are adapted to soft substrate, while others prefer to settle on hard substrate (Bayer 1961), so octocorals can be expected under different sedimentary conditions, too.

The deep-water octocoral biota off Mexico's entire Gulf coast should be a priority for future research. Rare genera occurred in the region (e.g., *Corallium* sp.), as well as species otherwise known only in the Straits (*Narella pauciflora*). The northwestern Gulf of Mexico also requires further attention. A single octocoral record (zone 8, 200 – 800 m) was directly adjacent to the third most diverse habitat in the Gulf of Mexico (zone 8, 50 – 200 m depth), so more octocorals would be expected. The zone ranks second only to the Straits of Florida in terms of octocoral diversity in the Gulf of Mexico.

If the estimate of 250 species is correct, one in every six species of octocorals are yet to be discovered. The Chao 1 estimator was a minimum predictor (Magurran 2004), so in actuality, total species richness may be higher. Discovery rates for the better-known scleractinians are steeply inclined, with no sign of asymptote (Cairns 2007). Knowledge of octocorals lags behind knowledge of Scleractinia (Bayer 1981) so it is reasonable to assume that expected richness for octocorals is high.

Documented richness (204 spp.) was higher than previously reported (185 spp.) for reasons unrelated to species estimation. The first reason was that our definition of species included unidentified taxa, i.e. specimens identified only to genus level. Our study characterized depth zones and regions, not valid species, so it followed that unnamed species should not be ignored. Octocoral data are limited, so all records should be maintained if possible. The two most commonly collected “species” were unidentified - *Acanella* sp. and *Thesea* sp. These species were important to regional and bathymetric characterization, but were not part of the species accumulation curves.

The accumulation did include 12 unidentified species in otherwise unrepresented genera. For example, *Paragorgia* sp. occurred twice in the Straits of Florida. These were the only records of the genus in the Gulf of Mexico. The assumption was that the colony was correctly identified to genus, but that no further effort went into the identification. Because we compared assemblage structure, it was immaterial whether the species were new or old, either way, richness increased by one, and a zone was better characterized. Unidentified species could be a problem if a genus were misidentified, or synonymies were present, but octocoral genera are distinct, and our taxonomic quality control measures were presumed to subsume established synonymies.

The second reason for the difference in documented richness was that our definition of the Gulf of Mexico is broad. The eastern boundary (80° W) encompassed the entire southern Straits of Florida. The boundary reached slightly into the West Atlantic, perhaps impinging on another biogeographic zone, perhaps including a few species adjacent to the Gulf that may not occur within the Gulf. Yet, range extensions are common for Octocorallia. For example, the bubblegum coral *Paragorgia* sp. was known from the Straits, but not the northern Gulf, until recent cruises (PJE, *pers. obs.*). There are few known endemics among octocorals. Many octocorals in the Gulf have distributions that extend to the Caribbean Antilles, and beyond, to Brazil. Theoretically, a minor adjustment of boundaries should be of little consequence.

Biogeographic provinces for octocorals were identified before. Deep octocoral provinces in the North Atlantic Ocean (Watling & Auster 2005) were found to share the affinities of deep scleractinians (Cairns & Chapman 2001). The current study compares well to analyses of long held theories of octocoral biogeography in the Gulf of Mexico. Our data generalize the shallow provinces more than previous studies, but find significant differences between depth zones. Giammona's (1978) analysis supported five shallow provinces (Bayer 1954) using techniques similar to ours, but he used fine-scale (1°) "subunits" with coarser taxonomic units (families) to emphasize regional assemblages at the expense of depth gradients. We emphasized depth zones and balanced sample sizes at the expense of regional resolution. As a result, our results support only a general shallow subdivision, with two biogeographic regions: a West Indian province to the east and south, and a Carolinian assemblage to the north (Bayer 1961). The benefit of our approach was that it provides evidence for extension of these provinces into the deep-sea.

Differences in octocoral diversity were not a primary focus of early work on the Gulf, but families and species were enumerated (Giammona 1978). Subunits with high family and species richness were consistent with our zones of high diversity. Highest richness was attributed to three of the six subunits that comprised the southern Straits of Florida - two subunits were in the south, on the Cuban side of the Straits near Havana, the other on the north side, corresponding with our zone 2, from 0 - 200 m (Giammona 1978). Total species richness for the Straits in Giammona's (1978) analysis amounted to 77 species following our quality control procedures. We documented 121 species in the Straits of Florida, 50 % more species. This may reflect better coverage in our report, but also perhaps an increase in the number of species described.

The Mississippi Delta subunit, east of the river (our zone 5) was found to be highest in family richness for the northern Gulf (Giammona 1978), a finding we might also support if depths < 800 m were combined into one subunit. Giammona (1978) documented 14 species of *Leptogorgia* and *Telesto* in his "subunit 11", along with sea pens, soft corals, and gorgonians. We listed 41 species in our zone 5, east of the Mississippi River, including all the aforementioned, plus several species in the Ellisellidae and Paramuriceidae. Between the Mississippi Delta assemblage and the Straits assemblage, species richness has nearly doubled in 30 years, but the ideas of two "hotspots" of diversity in the Gulf of Mexico were consistent between studies.

Giammona (1978) identified three octocoral assemblages in the Gulf, consistent with earlier studies: a warm-water group of Gorgoniidae and Plexauridae, a carbonate bank assemblage, and a deep-water octocoral assemblage. We were able to add resolution to this classification. We characterized the bank assemblage as a mid-depth group of

Ellisellidae and Paramuriceidae that extends from South Texas to the Straits. The deep-water assemblage was a diverse group that is likely to vary by substrate. Gorgonians in the Isididae, Chrysogorgiidae, and Primnoidae would be expected on hard substrates. Anthothelidae, Coralliidae and Paragorgiidae were also present. Sea pens in the Funiculinidae, Umbellulidae, and Virgularidae would be expected on soft substrates.

There was good agreement between the species assemblage described for the West Indian province (Bayer 1961), and the assemblage that characterized our eastern (West Indian) region. Bayer cited *Pseudopterogorgia*, *Pseudoplexaura*, *Eunicea*, *Plexaurella*, and *Muricea* as characteristic West Indian genera. Our analyses also ranked Gorgoniidae (*Pseudopterogorgia acerosa*, *Leptogorgia virgulata*, *L. hebes*) and Plexauridae (*Eunicea* spp., *Plexaurella nutans*, and *P. fusifera*) as characteristic species. *Telesto sanguinea* and *T. flavula* were common along West Florida (Bayer 1961). *T. sanguinea* placed 18<sup>th</sup> on our list for the West Florida shelf (zone 3), and third on the list in northwest Florida (zone 4), below *Leptogorgia* spp.. So, minor discrepancies occurred.

Typical Carolinian species reported for the northern Gulf were *Anthpodium rubens*, *Muricea pendula*, and *Leptogorgia hebes*. The latter *Leptogorgia hebes* was reported to occur along most, if not all, of the Gulf coast of Florida and west to Texas (Bayer 1961). Our study found no records of *A. rubens*, but *Leptogorgia* spp. were prevalent. *Renilla muelleri* and *Virgularia* sp. sea pens also characterized the shallow northern Gulf. Our characterization compares well to Giammona's (1978) "subunits", smaller boxes of 1° latitude and longitude showing plexaurid and gorgoniid species in the eastern Gulf, with *Leptogorgia* spp. predominant in the northern Gulf. We identify the

faunal transition in terms of decreased diversity and abundance west of Florida, associated with the loss of tropical families.

The reasons underlying the faunal transition in sample collections from the East and North could be related to differences in the nutrient, salinity, and sediment regime with increased proximity to the Mississippi River. *Leptogorgia* tolerates low salinity and low temperatures (Bayer 1961). The prevalence of sea pens in sample units from the North was also noted, from the shallows to the deepest zone. Sea pens are well adapted to soft sediments, so they should be adapted to substrate near the Mississippi River. Most gorgonian octocorals require hard substrate to settle. The absence of plexaurids and gorgoniids in sample units from the North can be explained by seasonal low temperature extremes, brought on by the passage of cold fronts associated with movement of the jet stream over Texas, November through March. Cold temperatures can diminish reef corals, tropical reef gorgonians should be similarly affected (Bayer 1961).

Three primary factors were proposed to influence the distribution of octocorals: (1) temperature, (2) substrate, and (3) depth (Bayer 1961, Giammona 1978). Each of these was invoked to explain our observations. Contrary to the suggestion that discharge from the Mississippi River has no effect the distribution of deep octocorals (Bayer 1961), we found depressed abundance and richness in samples from zone 6, adjacent to the river, to a depth of 800 m. *Leptogorgia* spp. and sea-pens were collected once or twice from shallow waters. *Muricea pendula* and various Paramuriceidae and Ellisellidae were collected once or twice from the mid-water. *Acanella* and *Callogorgia* were collected from the deep-sea, but again in low numbers. Richness was low relative to adjacent

zones. This could be a reflection of research effort, or perhaps related to sediment flux, salinity, and/or turbidity currents.

Oxygen content has not been considered as a factor in octocoral distribution. The Mississippi River outflow is known to induce a seasonal hypoxic “dead zone” on the continental shelf (Rabalais et al. 1996). The hypoxic zone was linked to low abundance of benthic macroinvertebrates (Pavela et al. 1983). Octocoral richness at 0 – 50 m was slightly higher in zone 7 than it was in zone 6. *Leptogorgia hebes*, *Muricea pendula*, *Sarcodictyon rubens*, and *Renilla muelleri* were reported within this hypoxic “dead zone.” Deep-sea isidid octocorals on North Pacific seamounts can be abundant in oxygen minimum zones (5% ml/l O<sub>2</sub>, Etnoyer 2008) so they appear to tolerate hypoxic conditions. Their sedentary lifestyle suggests oxygen requirements would be low. Low oxygen could even provide advantage if mobile predators were limited.

A common expectation for GIS- based analyses is to find a correlation between the presence of hard bottom substrate and benthic megafauna. Depth is one commonly recognized factor influencing species distribution (Sanders 1968), but substrate is another, particularly in the Gulf of Mexico, where major features like the Sigsbee Escarpment off Florida and the Mississippi Canyon clearly influence the distribution of species. We did not pursue the correlation between substrate and species abundance because substrate is not consistently reported for museum specimens. Geological classifications must be applied post-hoc by overlaying data coordinates on geological data layers in a GIS (Bryan & Metaxas 2007). Generalization of coordinates makes the association of substrate and collection locale difficult, because 1/100th of a degree will offset points by ~1 km. Even if coordinates are accurate, the low resolution of basin scale

data (100 – 1000 m) is only a rough approximation. Habitat forming substrate for deep octocorals in the Gulf of Mexico is often authigenic carbonate, large slabs on the scale of 1 – 10 m, with soft sediment between them, so misclassification is likely at coarse scales. To avoid spurious results, habitat associations (slope, substrate) should only be construed at site-scale, using high-resolution multibeam bathymetry and side-scan sonar, collecting substrate samples concurrently with voucher specimens.

We employed a very simple scheme, with variables for depth and location, hoping to garner information without inducing unnecessary error, or spurious effects. We found highest diversity and highest rates of species accrual from 50 - 200 m depth, on the upper slope. The next highest rate of accrual was 200 - 800 m on the mid-slope, but average diversity was not significantly different than shallower depth classes. A mid-slope peak in diversity is consistent with a pattern reported for bivalve mollusks and polychaete worms in the North Atlantic (Sanders 1968) and a unimodal peak in diversity in the mid-to lower bathyal zone, decreasing in the abyss (Rex 1983, McClain et al. 2008).

Two disjunct regions of the Gulf of Mexico had exceptional diversity of octocorals- the southern Straits of Florida and the northern Gulf of Mexico. The Straits were exceptionally rich to a depth of 1600 m, while the northern Gulf was richest 50 - 200 m. In the northwest Gulf of Mexico, the high diversity zone was restricted to the upper continental slope, in two zones 100 to 300 west of the Mississippi Canyon. Numerous salt diapirs underlie more than 100 banks of moderate (50 – 150 m) relief along the slope trend (Rezak et al. 1985). The banks and their surroundings appear to be high quality habitat for octocorals in the Ellisellidae and the Paramuriceidae. More than 5000 colonies are photo-documented in the region (Chapter 2) but faunal richness for the

region was better represented in the historical database (39 spp.). Evenness was high, and Simpson's diversity was also high.

The proximate cause for the exceptional diversity of the region was high species and genus richness in the representative families. *Nicella* and *Thesea* account for 20 species. The genera were surpassed only by gorgoniid *Leptogorgia* in richness. Many genera in the Ellisellidae and Paramuriceidae appear to be well suited to the slope environment, where they are abundant (Chapter 2). Their depth range is centered on the upper slope. *Ellisella*, *Nicella*, *Thesea*, *Scleraxis*, and *Bebryce* have mean depths of approximately 125 m. *Placogorgia* (225 m) and *Villogorgia* (195 m) are slightly deeper. Paramuriceidae are not well known, and most knowledge is from species descriptions in the Gulf of Mexico (Deichmann 1936), North Atlantic and Mediterranean Sea (Grasshoff 1977). Together, Ellisellidae and Paramuriceidae comprise a distinct Gulf assemblage according to Bayer (1961).

We speculate that the ultimate cause of the high relative diversity of the northern Gulf region was related to habitat quality, heterogeneity, productivity, and/or some combination of these effects. Outer Continental Shelf (OCS) banks of the Gulf of Mexico have 50 m relief on average, rising above the surrounding soft sediments to serve as substrate for settlement and growth. The peaks of most OCS banks are below the depth of the mixing layer (approximately 70 m; Rezak et al. 1985), so they are isolated from warm water temperatures that may set an upper limit on deep-water fauna (Cary 1918, Bayer 1961). Each feature is geologically unique, with slopes, fractures, and grabens at different exposures, and different depths. Where banks are absent, small relief topography (4 - 10 m) provides suitable settlement substrate, so heterogeneity is high. Their position on the

upper continental slope may be suitably intermediate, just far enough from the Mississippi River to be isolated from suspended sediments and hypoxia, but close enough to benefit from primary production associated with nutrient runoff.

Why was octocoral diversity so high in the southern Straits of Florida? Highest richness occurred in zone 2 in shallow and mid-water. The deep-sea depth range 200 – 800 m in zone 2 also ranked high. Steep escarpments characterized the topography to the north and south, bordering Florida and Cuba. The unique character of the Straits' assemblage was largely responsible for the persistent data structure (Fig. 6), because the assemblage was consistently different from samples at similar depths in the Gulf. Zone 13, the Yucatan Channel, was one exception. Zone 13 also ranked highly (number 6) among the top 10 most diverse sample units in the Gulf.

The proximate cause of high octocoral diversity in the Straits was geography. At low latitudes far to the east, the region was protected from cold winter temperatures that may limit the northern extent of shallow West Indian fauna like sea rods (*Eunicea* spp.) and sea plumes (*Pseudopterogorgia* spp.). Tropical genera (e.g., Gorgoniidae) are speciose, more so than Paramuriceidae. Shallow species are typically zooxanthellate, limited by depth of light penetration. However, in clear waters, Gorgoniidae can grow deeper than 50 m, so their richness would penetrate into the 50 – 200 m zone. The shallow Mexican coast is equally rich because of the tropical climate (Jordán-Dahlgren 2002, Nelson et al 1998). Tropical geography does not explain deep octocoral diversity, or its breadth through the Straits.

We speculate that the ultimate cause of high octocoral diversity in the Straits is linked to the interaction of steep topography and persistent water flows, which would

manifest high habitat availability and high habitat quality for octocorals. The Pourtales Terrace has been described as a broad expanse of high-relief, hard bottom habitat covering 3500 sq km in water depths 200 – 500 m (Reed et al. 2005). The West Florida Escarpment reaches a southern terminus in the western part of the southern Straits of Florida (zone 3), and this too, is characterized as complex topography, from 100 – 3000 m, notched by canyons with steep headwalls and deep terraces (Twichell et al. 1991).

Large volumes of water (30 Sv) funnel through these habitats in the form of the Florida Current, and these flows penetrate deeply (Schmitz & Richardson 1968). The Gulf of Mexico is the primary source, but passages through the Florida reef tract also contribute to the flows (Schmitz & Richardson 1991). The strength of the current is sufficient to prevent more than a thin veneer of sediment from accumulating (Gomberg 1976), so bedrock should be exposed to new recruits. Particle flux through the Straits should be high, and conducive to octocoral growth (Peccini & MacDonald 2007).

The question of differential research effort must also be addressed. The Straits of Florida benefit from proximity to Harbor Branch Oceanographic Institution, whose Johnson Sea –Link submersibles logged more than 50 dives in the Straits. The northern Gulf is a major source of oil and gas, where the Minerals Management Service has sponsored a good deal of research, too. Effort is high in several deep parts of the Gulf, except for the southern parts. Certain zones clearly suffer from low effort, e.g., the 200 – 800 m in zone 8. However, depressed richness and abundance would not be expected near the Mississippi River if effort were high, so these patterns may be justified. Simpson's diversity metric was insensitive to rare species, so it should be robust to differences in sample size between zones (Carney 2007).

More records and better areal coverage were used than in previous studies, but how well do the assembled octocoral data truly represent the fauna in the Gulf? This should be considered carefully, because some species known to be common were rare in our records. Accuracy of representation has an important bearing on the interpretation of some unexpected results; specifically, that deep octocorals were more commonly curated in museums than shallow-water taxa. Prevalence of deep-water species was an unexpected result. If relative frequency of collection accurately reflects relative abundance, then *Acanella* spp. and *Thesea* spp. occur more commonly in the deep sea than *Leptogorgia* sp. and *Pseudopterogorgia* sp. occur in shallow water. This is important because octocoral assemblages are a common shallow water habitat, so deep octocorals would be even more common.

There are explanations why deep octocorals may be collected disproportionately. Shallow water species may be more familiar, so there would be less need to collect them. Researchers may assume that they are already well represented in museum collections, and forego the opportunity to collect. Or, they may be collected frequently, but not vouchered for similar reasons. Alternatively, few other organisms are available to collect in deep water, so octocorals are taken preferentially. The novelty of deep octocorals may be high enough to warrant an excess of samples, but it seems counterintuitive that collection effort would be highest in deep water.

Shallow octocorals were well represented in the database, especially in Florida. Common shallow octocorals were commonly curated. *L. setacea* and *Ps. acerosa* ranked highly in Table 2. This was evidence against the hypothesis of familiarity. The concept that deep octocorals are collected preferentially still may hold merit, but it applies equally

to shallow water. Sponges and octocorals are conspicuous reef fauna. We hypothesize that the best explanation why deep octocoral records are more frequent than shallow water octocoral records is simply because deep corals are more abundant. The logical extension of the argument is that deep-water octocoral assemblages are a common habitat type in the deep Gulf of Mexico, because most of the seafloor is deeper than 50 m.

However, this presents a problem, because gorgonians dominate occurrences. Gorgonians require hard substrate to settle, but hard substrate is considered rare in the Gulf of Mexico; the deep-seafloor > 300 m is dominated by fine-grained sediment (Coleman et al. 1991). A common habitat type on an uncommon substrate would seem impossible. However, the nature of a patchy environment is that frequency of occurrence may be high, even if areal coverage is not. Deep-sea fans are reported from a variety of substrates, including natural hard-bottoms, such as lithohermes on the West Florida shelf (Reed et al. 2005, 2006) and authigenic carbonates associated with hydrocarbon seeps (Schroeder 2007, Becker et al. 2009); as well as artificial hard-bottoms, such as shipwrecks (Schroeder 2007), and oil rigs (J Reed, HBOI, *pers. comm.*) A variety of substrates and a range of adaptive capabilities may facilitate the broad distribution of octocorals in the deep Gulf of Mexico.

In conclusion, octocorals are rich, diverse, and presumably abundant in the deep Gulf of Mexico. Deep octocoral habitat types are also diverse, including, but not limited to: (1) shallow southern and eastern reefs, (2) northern Gulf and South Florida banks and mounds of low to moderate relief, (3) steep escarpments with a rich assemblage of gorgonians to 1600 m depth, and (4) patchy authigenic carbonates associated with hydrocarbon seeps. A comprehensive overview of octocoral depth and distribution is

provided that confirms long held theories of two biogeographic regions in the Gulf of Mexico (Bayer 1961, Giammona 1978), and extends these provinces into the deep sea. Two epicenters of high diversity for octocorals are mapped, each with different habitat characteristics and different octocoral assemblages.

In the future, broad scale collections are recommended in the southern and northern Gulf of Mexico to supplement the information collected. Taxonomic studies are warranted because common genera are poorly known, and associated species would be expected. Site scale investigations are recommended to quantify habitat associations, as the octocorals are clearly adapted to a broad range of conditions, as evidenced by their broad vertical distribution and remarkable richness.

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## CHAPTER TWO

Diversity of Mesophotic Octocorals in the Flower Garden Banks Region,  
Northwestern Gulf of Mexico

by

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Running head: Diversity of mesophotic octocorals

Key words: octocoral, alcyonacea, deep-water, diversity, distribution, Gulf of Mexico,  
banks, topographic features

## Diversity of Mesophotic Octocorals in the Flower Garden Banks Region, Northwestern Gulf of Mexico

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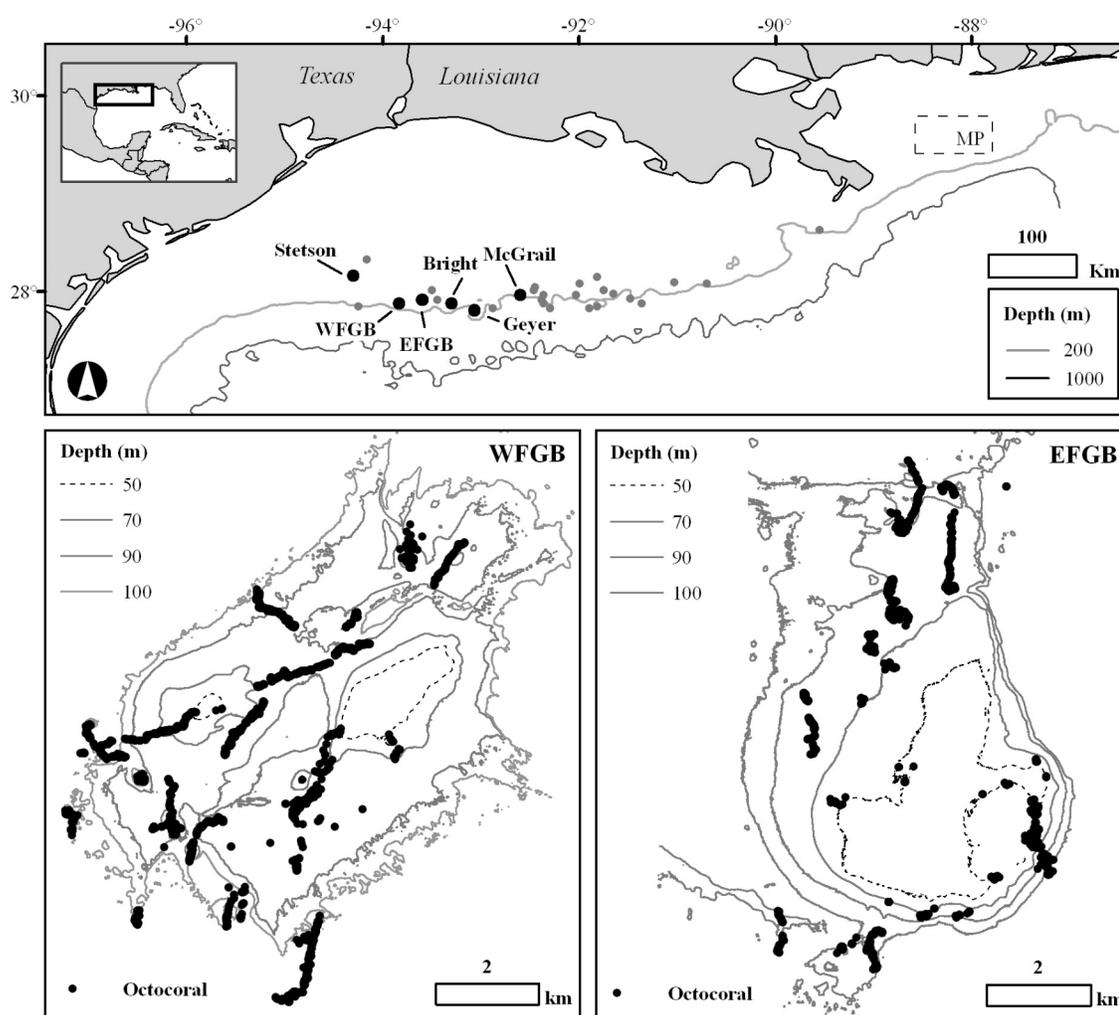
**ABSTRACT:** Octocorals are common and conspicuous on shallow reefs in the southern Gulf of Mexico, but they are absent from the coral reef caps of East and West Flower Garden Banks (EFGB, WFGB), occurring only in deep water (>50 m). Manned submersible surveys in the 1970's revealed a diverse assemblage of octocorals on WFGB and other northwestern Gulf banks. Since that time, 131 remotely operated vehicle transects were conducted on six banks aboard 12 research cruises from 2001-2005. Octocorals were collected and identified. A geo-referenced photo database of 5408 in-situ images 50 – 150 m depth was cross-referenced to voucher specimens. No octocorals occurred shallower than 50 m. Data were imported to a Geographic Information System at the genus level. Octocoral assemblages were comprised of a shallow group (*Swiftia*, *Diodogorgia*, and *Muricea*) and a significantly deeper group (*Ellisella*, *Nicella*, *Hypnogorgia*, *Caliacis*, *Thesea*, *Chironophthya*, and *Callogorgia*). Total richness and abundance was highest on WFGB and EFGB, but Simpson's diversity was highest on Bright Bank, a relatively unexplored feature. Richness was significantly positively correlated with research effort. Low relief substrates (2 – 30 m) between banks accrued genera nearly as rapidly as the richest banks. This was unexpected; the implication is for a broadly distributed habitat type in the northwestern Gulf. A checklist is provided for 24 species on EFGB, WFGB, and surrounding banks, with plots of relative abundance, genus accrual, and depths of occurrence for 13 deep-water octocoral genera.

## INTRODUCTION

Like many marine protected areas around the world, Flower Garden Banks National Marine Sanctuary (FGBNMS) encompasses substantial deep-water habitat (> 50 m) that is under-explored relative to shallower depths within recreational and scientific scuba diver depth range (< 40 m). Octocorals are common and conspicuous benthic megafauna on banks in the northwestern Gulf of Mexico (Rezak et al. 1985). They are well adapted to cold, dark-water environments down to 5850 m (Cairns & Bayer 2009a). Octocorals (soft corals, sea fans, sea whips, sea pens) are broadly distributed on continental shelves and slopes throughout the world's oceans wherever suitable substrate exists (Bayer 1961). They create structural complexity in a relatively featureless environment, generating habitat for associated species of fish (Heifetz 2002, Etnoyer & Warrenchuk 2007), invertebrates (Krieger & Wing 2002, Buhl-Mortensen and Mortensen 2005), and microbial fauna (Penn et al 2006). For better management it is important to understand and characterize these deep-water benthic assemblages.

The mesophotic depth range (50 – 200 m) has been called the “Twilight Zone” because light is diminished (Frick & Knauer 1986), but also because it is out of reach, too shallow for research submersibles, but too deep for scientific diving. Some biologists refer to the mesophotic zone as a new frontier, because it represents a knowledge gap that renewed interest in deep-water technology is now beginning to fill (Pyle 1996). Many topographic features punctuate the mesophotic zone in the northwestern Gulf of Mexico. The banks provide substrate for octocorals in the Ellisellidae and Paramuriceidae (Rezak et al. 1985). Knowledge of species are limited, primarily restricted to species lists and species descriptions. Little is known of their diversity and distribution.

The boundaries of FGBNMS encompass three topographic features. Stetson Bank is a claystone/siltstone outcrop in 30 – 60 m of water on the continental shelf in the northwestern Gulf of Mexico (Lankford & Curry 1957). West Flower Garden Bank (WFGB) and East Flower Garden Bank (EFGB) are two uplifted salt dome features 20 – 120 m deep, situated on the continental shelf break about 200 km southeast of Galveston (Fig. 1). A large complex of more than 50 salt dome features is situated along the outer continental shelf (OCS) between FGB and the Mississippi Canyon (Rezak et al. 1985).



**Figure 1. Banks in the northwestern Gulf of Mexico.** Top- Map of outer continental shelf banks discussed in the text (black dots) and other recognized banks (gray dots). Bottom - Octocoral occurrences (> 50 m, black dots) overlaid on detailed bathymetry of West Flower Garden Bank (WFGB) and East Flower Garden Bank (EFGB) (Gardner et al. 1998).

The banks are productive fishing grounds for grouper, snapper, amberjack, and mackerel, visited often by fishers and recreational divers. Bright, Geyer, and McGrail Banks are within 100 km of sanctuary boundaries, but only McGrail Bank and FGBNMS reef caps shallower than 50 m support vigorous coral reef growth (Schmahl & Hickerson 2006).

The coral reef caps on EFGB and WFGB are the northernmost true tropical reefs on the continental shelf of North America (Rezak et al. 1985). They are known among biologists as some of the healthiest reefs in the West Atlantic, noted for annual lunar synchronous spawning events (Gittings et al. 1992, Hagman & Vize 2003, Vize 2005), high-coral cover (Schmahl et al. 2008), and low incidence of disease (Gittings 1998, Aronson et al. 2005). These mid-latitude reefs (20° N) are distinguished from other reefs to the south and east by: 1) an apparent lack of corals in the genus *Acropora* (until recently, see Zimmer et al. 2006) and 2) the complete absence of Alcyonaria within scuba diver depths (Rezak et al. 1990).

Seafloor habitat just below the reef cap (45 – 90 m) is an algal-sponge zone dominated by coralline algae (Rezak et al. 1985). Near 70 m, this becomes a transition zone characterized by an azooxanthellate assemblage of soft corals and black corals well adapted to diminished light levels (Schmahl et al. 2008). The deep-reef communities are nearly as diverse biotically as the coral reefs (Rezak et al. 1985).

Deep-water explorations of the northwestern Gulf of Mexico banks from 1974-1980 using the *Diaphus* submersible to 210 m found terraces, and ridge like features, also called “drowned reefs” on WFGB near 100 m depth. The features were characterized as sea fan habitat (Rezak et al. 1985), though an entire volume describing the biota of the bank mentions only one sea fan, in a photo of the gorgonian *Placogorgia* sp. (Bright &

Pequegnat 1974). Deep EFGB and WFGB were described as an Antipatharian Zone from 60-90 m, adjacent to a deeper drowned reef zone covered with a veneer of fine sediment, bearing a low diversity epifaunal community, including octocorals (Rezak et al. 1985).

Alcyonarians were most abundant 70 – 80 m. Taxonomic resolution was low in the habitat description, identified as Ellisellidae and Paramuriceidae, but 27 species were included in the species list for the region (Rezak et al. 1985). The list was generated from samples collected on the southeastern banks (Bright, Diaphus, Geyer, Elvers, etc.) not FGBNMS. Octocoral species from FGBNMS were included in a few reports (Deichmann 1936, Giammona 1978), but not treated in any comprehensive manner.

Nearly 150 remotely operated vehicle (ROV) dives were conducted by FGBNMS staff using different ROVs and submersibles to 140 m depth during 12 research cruises from 2001-2005 called the Deep Fish Habitat (DFH) expeditions. The primary objectives of the FGBNMS DFH expeditions were to: 1) assemble a comprehensive species list of marine fauna within sanctuary waters, and 2) map megafaunal distribution by cross-referencing species identifications for voucher specimens to a geo-referenced photo database of in-situ images.

A geo-referenced photo-database of 8500 images was assembled for six major topographic features along the shelf break. Seafloor images were tagged with genus and species names to facilitate analysis of benthic megafauna and their distribution. Octocorals were relatively conspicuous, and a focus of collection, so the group was well represented in the database. Octocoral samples were used here to provide a preliminary list of species in the region and prioritize future work, while the photo-geodatabase was used to analyze diversity and distribution at the genus level.

The primary research questions addressed in this manuscript are: What species of octocorals can be found in the FGBNMS and on the surroundings banks? Which are most common, and most rare? Are there differences in vertical ranges between genera? Are there differences in the diversity of octocoral assemblages between banks? And, can these differences be explained by research effort? The fundamental intention is to determine whether the FGBNMS deep-water octocoral assemblage is the same as or different from octocoral assemblages in other deep-water sites in the Gulf of Mexico.

## **MATERIALS AND METHODS**

Seven research expeditions on and between banks in the northwestern Gulf of Mexico 2001-2005 used consistent photo-documentation protocols. Research effort was uneven, reflecting a hierarchy of research priorities for FGBNMS. Photos were collected with a Scorpio 3.2 megapixel digital camera (Insite Pacific) mounted at an oblique angle on the National Undersea Research Center's (NURC) Phantom S2 ROV. The photo-documentation method was exploratory. The primary goal was to investigate new habitat. Photos were not random. Photo-locations were chosen to represent the conspicuous epifauna and to characterize the benthic habitat in a qualitative manner. Animals selected for photography included corals, fish, crabs, algae, echinoderms, and sponges. Experts for each taxonomic group provided species identifications using voucher specimens. Voucher specimens were used to identify taxa within 8495 benthic images, if present. Sanctuary staff familiar with the benthic megafauna tagged each image with the species identification based upon determinations made by the taxonomic authorities.

Each of 8495 DFH photo records in the assembled geodatabase includes fields for vessel name, cruise and dive number, photo name, latitude, longitude, observed (ROV) and multibeam depth in meters, followed by a list of octocoral genera with values for the number of colonies per photo (1 – 90). Data are prevalence, not incidence, because more than one colony can occur in any image. Photo coordinates were derived from ultra short baseline navigation ( $\pm 10$  m horizontal accuracy) using decimal degrees to the sixth decimal point. ROV depth readings were derived from a strain gauge pressure transducer buffered to 1mv per foot of seawater. Depth was displayed on the video overlay in feet.

Observed (ROV) depth values are available for  $\sim 1/3$  of the field records. Missing values were supplanted by depth values from high-resolution (4 m) multibeam from the United States Geological Survey (Gardner et al. 1998, Gardner & Beaudoin 2005) in a geographic information system (GIS) using the “extract values to points” function in the ArcGIS 9.2 Toolbox (ESRI 2008). Multibeam (MB) depth values were accurate within 5 m of observed depth values 70% of the time, and within 10 m 90% of the time. Vertical distribution plots of octocoral genera use observed depth values exclusively, except the genus *Muriceides*. Multibeam depth values were used to augment sample sizes for univariate tests, and to subset 8495 images to 5408 unique images deeper than 50 m.

Only one or two specimens from each distinct morphotype were typically collected for species identification. Octocoral colonies were photographed in-situ before they were collected. A subsample was clipped from the colony and photographed under the dissecting microscope in ambient seawater before preservation in 90% ethanol. Some specimens were kept in FGBNMS archives, but the most were submitted to natural history archives, museums, and collections in order to distribute the material, and to

access the expertise of several leading authorities in octocoral systematics. Drs. F. M. Bayer and S. D. Cairns identified specimens submitted to National Museum of Natural History (NMNH), and Dr. G. C. Williams identified specimens submitted to the California Academy of Sciences. Some colonies were identified only to genus. Sclerite plates were produced for most specimens, and compared to published literature.

Sclerite plates were prepared using standard laboratory techniques described in laboratory notes by F. M. Bayer (Smithsonian Institution NMNH, *pers comm*). Polyp tissues were dissolved in a diluted sodium hypochlorite solution (commercial bleach) in a small glass 5 ml beaker and the solution drawn away by pipette. The remaining calcitic sclerites were cleaned by successive rinses in hydrogen peroxide solution, distilled water, 70% ethanol, and 95% ethanol, then mounted on sticky stubs for gold plating. Scanning electron microscope (SEM) images were generated using the AMRAY 1810 at NMNH and Zeiss EVO 40 XVP at Santa Barbara Museum of Natural History. Individual sclerite images were masked and merged into plates of representative sclerite forms using Adobe Photoshop CS software. Plates were compared to sclerite illustrations from Deichmann (1936), Bayer (1961), and SEMs from Grasshoff (1977). The resulting identifications were then applied to all images depicting similar morphotypes.

Trained individuals can identify photographed octocorals to genus with some degree of consistency and accuracy, but identifications of species are extremely difficult, even with samples in hand. Octocoral species can rarely be discerned from photographs unless certain characters (e.g., color, polyp arrangement) are obvious. Species in the genus *Nicella* are notoriously difficult to distinguish, even under a microscope (Cairns 2007). So, depth and distribution analyses were conducted at the generic level to

minimize species-level identification errors. The classification affects only three genera with more than one species – *Ellisella*, *Hypnogorgia*, and *Nicella*. *Placogorgia* does not occur in the database, only in the species list.

Datasheets from each of 131 ROV dives were standardized, formatted, and concatenated into a single database of 5048 unique images > 50 m using Microsoft Excel. Octocoral species were selected from the multi-taxa framework, binned to genus, and imported to ArcGIS 9.2 (ESRI 2008) as a point feature with attributes for vessel name, site name, cruise number, dive number, location, photo name, observed depth, multibeam depth, and octocoral genus. Attributes for geology and biology were not assimilated. The resulting GIS point feature was defined geographically using the WGS 84 datum and projected into UTM Zone 15N, consistent with multibeam bathymetry (Gardner et al. 1998, Gardner & Beaudoin 2005). Point coordinates were overlaid onto 4 m and 10 m resolution multibeam echosounder data to import and assess multibeam depth values.

Some statistical assumptions were violated, particularly because photos were non-random. Octocorals did not occur in every image. Only 27% of images depicted octocoral colonies. Null data were available in deep and shallow water. Photos were treated as independent because duplicate and replicate images were removed. Analysis proceeded under the rubric of a meta-analysis, since data were not collected for the purposes of our research questions. The approach was justified because research effort was exceptional (nearly 50 days of mapping and 85 days of ROV work), and no comparable data were available to answer the research questions with appropriate taxonomic resolution. Video was not employed because high-resolution was necessary to discriminate between genera.

The intention of the study was to qualify and compare octocoral assemblages, not to discern habitat quality, so the approach was deemed acceptable.

The research design had two aspects. In the first aspect, the octocoral genus was treated as the independent variable and depth was the dependent variable. Wilkes test was used to check normality in depth distribution values, and Kruskal-Wallis was used to test for differences. A modified Scheffe's Test for unequal sample sizes was used to test for pair-wise differences between genera. In the second aspect, banks were treated as independent, and genera as dependent, in order to compare rates of genus accrual and diversity by bank. A sample-based rarefaction technique "Mau Tau" was employed in EstimateS8 software (Colwell 2006), randomized and recomputed 50 times, to compare rates of accrual between banks with different sample sizes with 95% confidence intervals (CIs) (Colwell et al. 2004). Sample-based rarefaction was preferred over other techniques (Carney 2007) because it preserves the ratio of species to individuals (Levin et al. 2001).

Diversity measures were calculated to understand how the composition of octocoral assemblages differs between sites. Diversity indices included Simpson's index in the form  $(1 - \lambda)$  and Simpson's evenness index ( $E_{1/D}$ ), the reciprocal form of Simpson's  $D$ , divided by richness (Smith & Wilson 1996). The latter was calculated to interpret the diversity measure in terms of its individual components, richness and evenness. Diversity calculations were performed in PRIMER 6.1 software (Clarke & Gorley 2006). Unequal sample sizes were addressed using a matrix of average abundance per photo for each genus at each site. Simpson's index is robust and meaningful (Magurran 2004), a more effective measure for ranking communities than rate of accrual (Lande et al. 2000).

Linear regression of generic richness and effort was performed to understand the effect of differential research effort on sample richness. Research effort was calculated by bank, in each of three forms: the numbers of photos per bank, the dives per bank, and the area searched. Area was calculated using minimum area polygons around ROV transects in the GIS, at the scale of the transect. The projection was UTM Zone 15 N, with datum WGS 84. Linear regression was also employed to identify the correlation between depth and richness in sample photos, using zero as a constant in Microsoft Excel. The resulting analyses provide a general overview of species richness, rate of genus accrual, and relative diversity of octocoral assemblages of six banks in the northwestern Gulf of Mexico, with consideration of the research effort that informed those measures.

## RESULTS

Twenty-four unique species in 16 octocoral genera were collected and identified from FGBNMS and surrounding banks. A checklist and classification are provided in Table 1 with the published depth range of occurrence and the depth range for this study. Octocoral genera were in seven families: five predominantly deep-water taxa (Anthothelidae, Ellisellidae, Keroeididae, Paramuriceidae, and Primnoidae) and two predominantly shallow-water taxa (Gorgoniidae, Plexauridae). Five specimens were not yet identified to species level, but are identified to genus. These were listed as “sp.” in the species column for *Hypnogorgia*, *Placogorgia*, *Swiftia*, and *Ellisella*. More samples and more research are needed to verify characteristics of species in these groups.

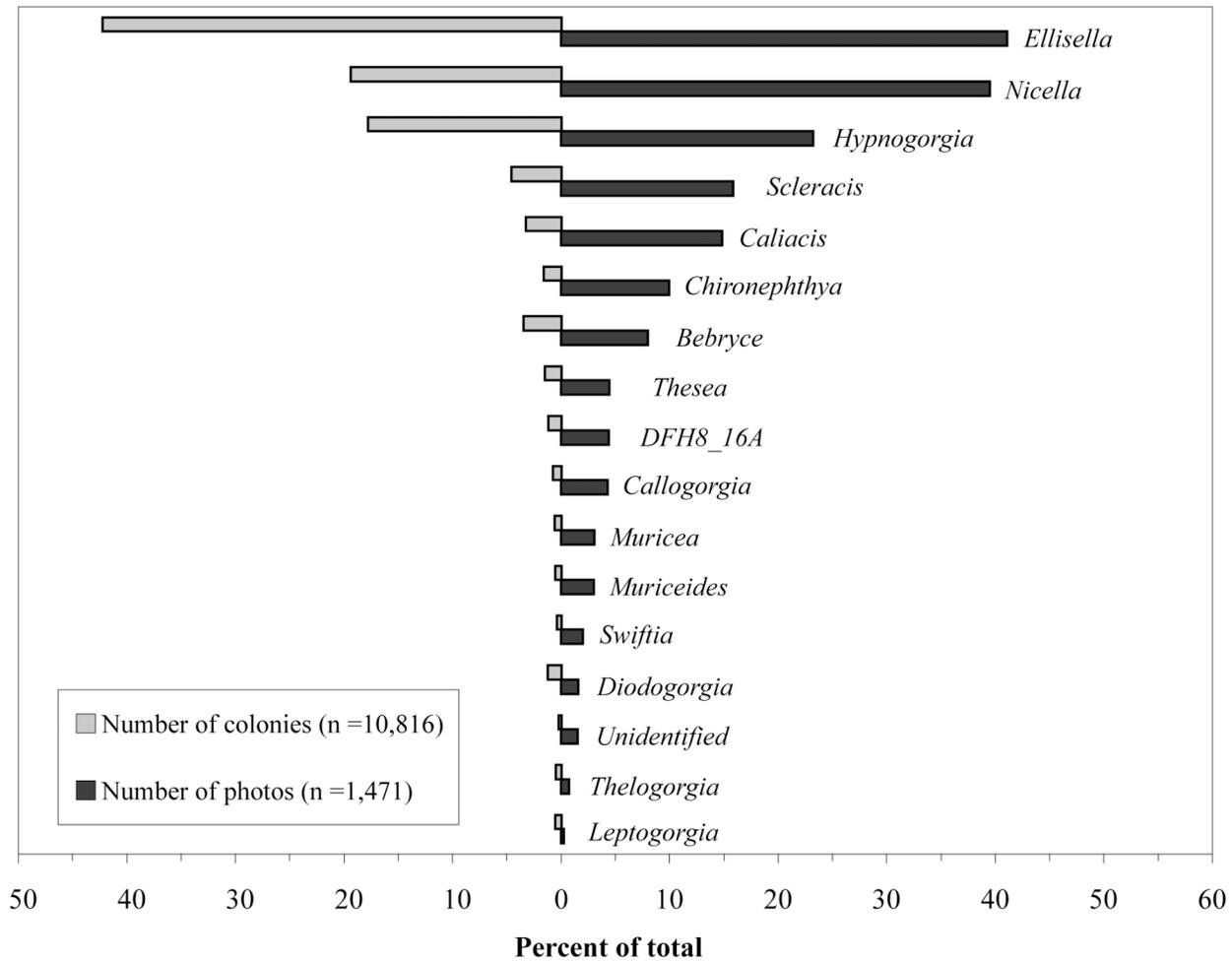
**Table 1. Checklist of octocorals collected from the Flower Garden Banks region** Columns indicate known depth range “Depth (m)” (Cairns & Bayer, 2009) and observed range “FGB (m)”. An asterisk indicates a range extension. The system of higher taxa is after Williams & Cairns (2006), but genera follow Wirshing et al. (2005).

		No.	Depth (m)	FGB (m)
ORDER ALCYONACEA				
SUBORDER ALCYONIINA				
<b>Family Nidaliidae Gray, 1869</b>				
Subfamily Siphonogorgiinae				
<i>Chironephthya</i> Studer, 1887				
<i>Chironephthya caribaea</i> (Deichmann, 1936)				
		1	16-183	74-121
SUBORDER SCLERAXONIA				
<b>Family Anthothelidae Broch, 1916</b>				
Subfamily Spongiodermatinae Aurivillius, 1931				
<i>Diodogorgia</i> Kükenthal, 1919				
<i>Diodogorgia nodulifera</i> (Hargitt, 1901)				
		2	30-183	63-80
SUBORDER HOLAXONIA				
<b>Family Keroeidae Kinoshita, 1910</b>				
<i>Thelogorgia</i> Bayer, 1992				
<i>Thelogorgia stellata</i> Bayer, 1991				
		3	62	95-104
<b>Family Paramuriceidae</b>				
<i>Bebryce</i> Philippi, 1841				
<i>Bebryce cinerea</i> Deichmann, 1936				
		4	64-274	80-104
<i>Hypnogorgia</i> Duchassaing & Michelotti, 1864				
<i>Hypnogorgia</i> sp. 1				
		5		
<i>Hypnogorgia</i> sp. 2				
		6		
<i>Muriceides</i> Studer, 1887				
<i>Muriceides hirta</i> (Pourtalès 1867)				
		7	53-592	52-130
<i>Placogorgia</i> Studer, 1887				
<i>Placogorgia</i> sp.				
		8		87
<i>Placogorgia mirabilis</i> Deichmann, 1936				
		9	53-185	87
<i>Placogorgia tenuis</i> (Verrill, 1883)				
		10	76-479	87
<i>Scleracis</i> Kükenthal, 1919				
<i>Scleracis cf petrosa</i>				
		11	62-1604	
<i>Scleracis guadalupensis</i> (Duchassaing & Michelotti, 1860)				
		12	51-120	
<i>Swiftia</i> Duchassaing & Michelotti, 1860				
<i>Swiftia</i> sp.				
		13	21-985	56-84
<i>Thesea</i> Duchassaing & Michelotti, 1860				
<i>Thesea rubra</i> Deichmann, 1936				
		14	120-837	80-102*
<b>Family Plexauridae Gray, 1859</b>				
<i>Caliacis</i> Deichmann, 1936				
<i>Caliacis nutans</i> (Duchassaing & Michelotti, 1864)				
		15	37-188	56-121
<i>Muricea</i> Lamouroux, 1821				
<i>Muricea pendula</i> Verrill, 1864				
		16	13-125	53-78
<b>Family Gorgoniidae Lamouroux, 1812</b>				
<i>Leptogorgia</i> Milne Edwards & Haime, 1857				
<i>Leptogorgia virgulata</i> (Lamarck, 1815)				
		17	3-82	70
SUBORDER CALCAXONIA				
<b>Family Ellisellidae Gray, 1859</b>				
<i>Ellisella</i> Gray, 1858				
<i>Ellisella</i> sp.				
		18		56-113
<i>Ellisella atlantica</i> Toplitz, 1929				
		19	24-214	
<i>Ellisella barbadensis</i> (Duchassaing & Michelotti 1864)				
		20	20-479	
<i>Nicella</i> Gray, 1870				
<i>Nicella deichmannae</i> Cairns and Bayer, 2002				
		21	27-403	68-123
<i>Nicella goreau</i> Bayer, 1973				
		22	45-110	
<i>Nicella guadalupensis</i> (Duchassaing & Michelotti, 1860)				
		23	62-311	
<b>Family Primnoidae Gray, 1857</b>				
<i>Callogorgia</i> Gray, 1858				
<i>Callogorgia gracilis</i> (Milne-Edwards & Haime, 1857)				
		24	82-514	91-117

The annotated checklist is not a complete account of octocoral diversity on the banks. Seven common morphotypes were coded, but not identified: G2 (n = 2), G5 (n = 6), G8 (n = 2), G9 (n = 5), G13 (n = 4), DFH8-16A (n = 43), DFH11-12A (n = 2). Other rare morphotypes were coded “Unid. color,” where “color” is red (n = 16), white (n = 4), yellow (n = 4), orange (n = 1), or purple (n = 1). The latter were grouped together as “*unidentified*” in the graphs of generic abundance provided in Figure 2. “Unidentified” octocorals occurred in 2% of the photographs, and comprised 0.20% of octocoral colonies. *Placogorgia* spp. and *Leptogorgia virgulata* Lamarck 1815 occurred in low numbers of photos (0, 3); they were excluded from depth analyses. *L. virgulata* was included in the checklist, graph of frequency (n = 3), and abundance (n = 56) (Fig. 2).

Three species not included in our species list are reported from FGBNMS (Deichmann 1936, Giammona 1978), but these were not collected during the DFH expeditions: *Siphonogorgia agassizi* Deichmann, 1936; *Thesea grandiflora* Deichmann, 1936; and *Riisea paniculata*, Duchassaing & Michelotti, 1860. Thus, the total number of documented octocoral species collected from FGBNMS is 24, but the true number of species present may be as high as 34, if all unidentified specimens prove to be unique and previously documented species are extant on the banks.

As many as 90 individual colonies were present in any single photograph, so relative abundance between genera differed depending upon whether the number of times the genus occurred in a photograph was compared (*frequency*), or the total number of colonies that occur in a photograph (*abundance*). Bar charts in Figure 2 illustrate both methods. *Ellisella* was the predominant benthic megafauna. *Ellisella* colonies occurred in 41% of photos with octocorals (n = 604), and accounted for 42% of colonies observed



**Figure 2. Relative abundance and frequency of octocoral genera.** Abundance (light gray bars) and frequency of observation (dark gray bars) for octocoral genera on Flower Garden Banks and surrounding features. “DFH\_16A” is a commonly observed morphotype. “Unidentified” groups five rarely observed morphotypes into one category. Frequency sums higher than 100% because more than one genus can occur in an image.

(n = 4557). *Nicella* colonies were the second most abundant (n = 2086 colonies), and the second most frequent (n = 581 photos). Together, *Ellisella*, *Nicella*, and *Hypnogorgia* accounted for 79% of colonies photographed. *Scleraxis* (16% of images) and *Caliacis* (14% of images) colonies occurred frequently, but not often in large numbers. Overall, octocorals were abundant, occurring once in every four photos ( $1471/5408 = 0.27$ ). Black corals and hard corals also occurred frequently.

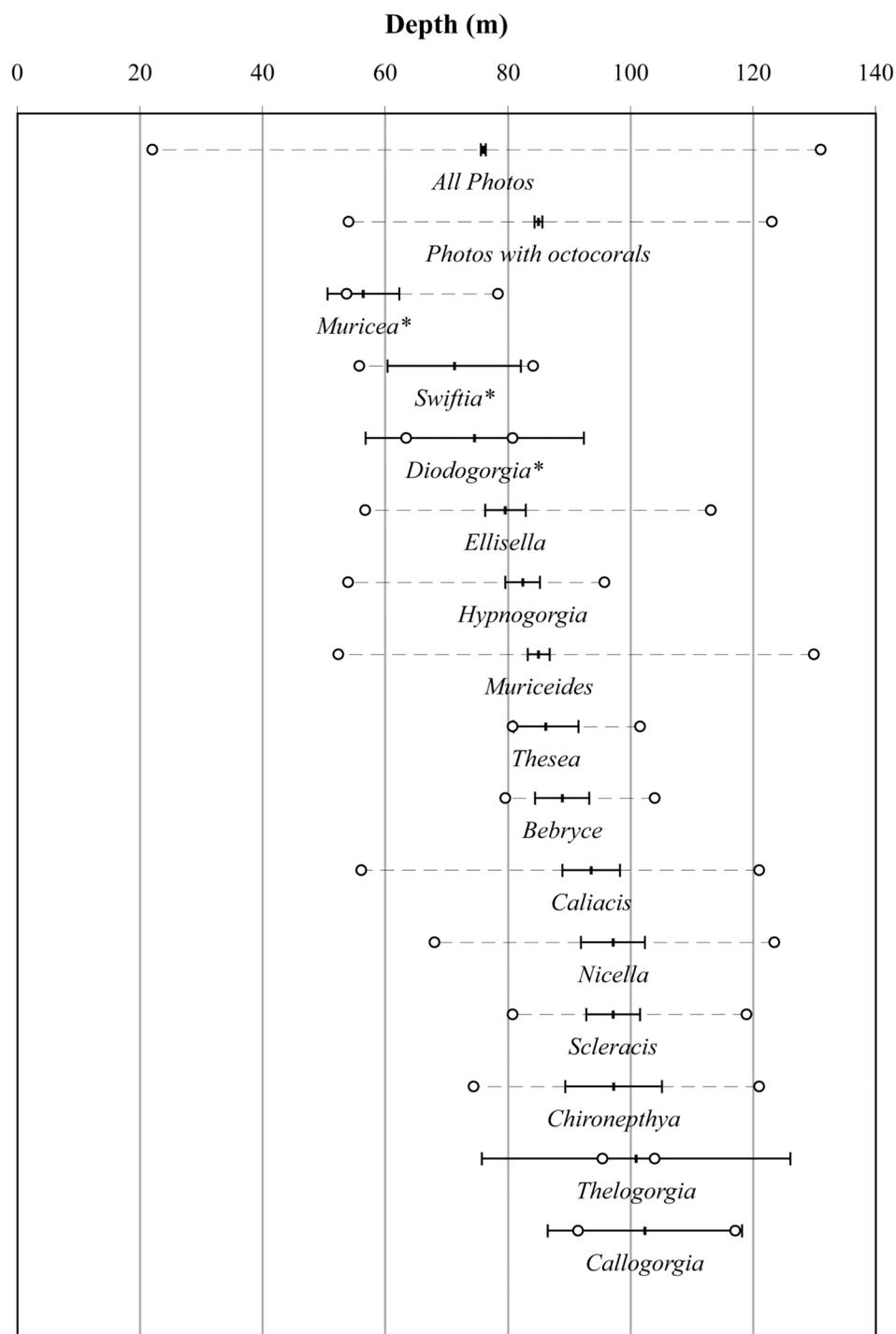
All FGBNMS octocoral species occurred within their published bathymetric ranges, except for two. *Thesea rubra* Deichmann, 1936 (n = 65 photos, n = 158 colonies) was found 20 m shallower than the species was known to occur elsewhere. *Hypnogorgia* spp. occurred to 96 m, slightly deeper than published estimates. Roughly half of the species collected are believed to occur exclusively in deep water (Cairns & Bayer 2009b). The most striking observation regarding depth distribution was that no octocorals were found shallower than 52 m. The same minimum depth applied to several taxa, including *Muricea pendula* Verrill, 1864, *Caliacis* sp., *Ellisella* spp., *Nicella* spp., and *Swiftia* sp..

Location explained the minimum depth threshold for two species, *M. pendula* and *Swiftia* sp., found almost exclusively on Stetson Bank. Stetson reached maximum depth at 55 m. The minimum depth threshold was not as easily explained at EFGB and WFGB. Considerable effort was invested in surveys shallower than 55 m. More than 600 photos (~20% of 2973) had observed depth values shallower than 55 m, and 3027 photos (~35% of 8495) had interpolated depth values shallower than 55 m. Recreational and scientific divers routinely perform reef-fish and coral surveys to 40 m in FGBNMS, but no octocoral sightings were reported in 25 years.

The mean depth for all photos (~75 m, n = 8495) was roughly in line with the mean depth for all octocorals. The sample sizes of species images with recorded depth values were: *Ellisella* (n = 248), *Nicella* (n = 140), *Hypnogorgia* (n = 181), *Scleracis* (n = 105), *Caliacis* (n = 105), *Chironephthya* (n = 50), *Bebryce* (n = 71), *Thesea* (n = 46), *Muriceides* (n = 0), *Muricea* (n = 26), *Swiftia* (n = 24), *Callogorgia* (n = 14), *Diodogorgia* (n = 9), *Thelogorgia* (n = 6). Depth ranges for genera were presented in the order of their average depth, from shallow to deep (Fig. 3).

Depth distributions were based on observed (ROV) values, except for *Muriceides hirta* (Pourtalès, 1868). Many images included *M. hirta* (n = 61), but no colonies were documented at the same time ROV depth was documented. *Callogorgia gracilis* (Milne-Edwards & Haime, 1857) and *Thelogorgia stellata* Bayer, 1991 colonies had the deepest mean depth values (100 m), but *Caliacis*, *Nicella*, and *Scleracis* averages were only slightly shallower. Standard errors were less because of larger sample size. The vertical range of the true soft coral *Chironephthya caribaea* Deichmann, 1936 was centered on the 100 m isobath. *Ellisella*, *Hypnogorgia*, *Bebryce*, *Thesea*, and *Muriceides* were shallower by 10 – 20 m, in moderate depths 80 – 90 m, while *M. pendula*, *Swiftia* sp., and *Diodogorgia nodulifera* Hargitt and Rogers, 1901 constituted the shallowest class of octocorals, 60 – 80 m deep.

Depth data were normally distributed (Wilkes  $\omega = 0.98$ ), but sample sizes were unequal. Scheffe's post-hoc test was used to identify differences between 16 octocoral genera (the 17 taxa in Figure 2, less *Leptogorgia*). Sample sizes in four genera were augmented by multibeam data. There was no difference between observed depth values and multibeam depth values (Mann-Whitney U test,  $p < 0.05$ ) when species with small



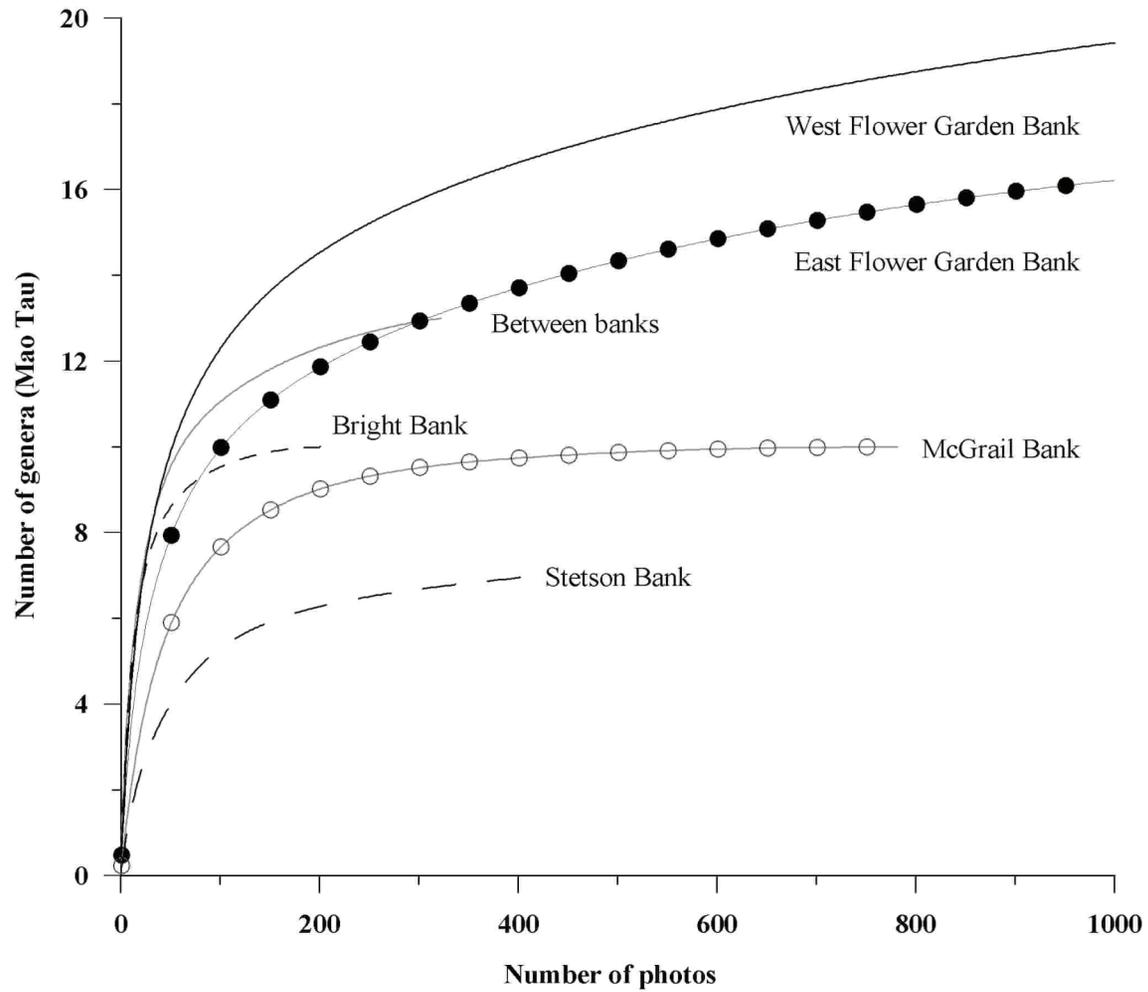
**Figure 3. Depth distribution of photo samples and octocoral genera.** Mean depth of observation in meters (small vertical dash) with one standard error (solid line, large vertical dashes) for photographs depicting each genus. Minimum and maximum depth of occurrence are the dashed line with circles. An asterisk (\*) indicates a depth range significantly different from others (Kruskal-Wallis,  $df = 13$ ,  $p < 0.05$ ; Scheffe's post-hoc test,  $df = 13$ ,  $p < 0.05$ ).

sample sizes ( $n < 10$ ) for observed depth (*C. gracilis*, DFH8-16A, *M. hirta*, *T. stellata*) were augmented by multibeam data to achieve larger sample sizes ( $n = 10 - 61$ ).

There was a significant difference (Kruskal-Wallis,  $df = 15$ ,  $p < 0.001$ ) in depth distribution between genera. The depth distributions for *M. pendula*, *Swiftia* sp., and *D. nodulifera* were different than all other taxa (Kruskal-Wallis,  $p < 0.01$ ; Scheffe's test,  $df = 15$ ,  $p < 0.05$ , see Appendix 2). This supports the idea of a shallow group, or assemblage, but *Muricea* and *Swiftia* distributions were also significantly different. The depth distribution of *Chironephthya caribaea* was different than the shallow group, *Ellisella* and *Hypnagogia*. The vertical range for *C. caribaea* was similar to others with mean values  $> 97$  m, including *C. gracilis*, *Nicella*, *Scleracis*, DFH8-16A, and *Unid*. This is notable because *C. caribaea* can occur as shallow as 16 m (Cairns & Bayer 2009b).

Octocorals were identified on all six banks (EFGB, WFGB, Stetson Bank, McGrail, Bright, and Geyer) and on two mud volcano surveys (Mud One and Mud Two) classified as "between sites". This area is now known as Horseshoe Bank as an outcome of the mapping and management activities of FGBNMS. One mud volcano (Mud Two) had a high generic diversity ( $n = 6$ ), but the other had only *Scleracis* spp. Octocorals were also documented over the course of three ROV transects in low relief areas between EFGB and WFGB, and upon low relief ring around Stetson Bank. No genus appeared to be completely indigenous to any bank, other than a relatively high frequency of *Muricea pendula* on Stetson Bank, which occurred only once on EFGB.

Rates of genus accrual were highest on WFGB and EFGB (Fig. 4), but confidence intervals overlapped (at  $n = 300$ ) with rates of accrual derived from transects between banks. Bright Bank had few samples, and few transects, but discovery rates were high.



**Figure 4. Genus accrual on northwest Gulf of Mexico outer continental shelf banks** Sample-based genus accrual curves (Mao Tau, Colwell et al. 2004) for each of six survey sites, randomized and recomputed 50 times. Geyer Bank is not shown (n = 91).

Stetson Bank and McGrail Bank had lowest rates of genus accrual. Geyer Bank was not included due to low sample size. Based upon confidence intervals (not shown), the most demonstrable differences in generic richness were between photo samples from WFGB (high richness) and McGrail and Stetson Banks (low richness). Confidence intervals overlapped in all other pair wise comparisons.

When morphotypes were treated as genera, photo samples from WFGB and EFGB ranked highest for genus richness, with 20 and 17 genera, respectively. Photo samples from sites between banks had moderate richness (11 genera), nearly the same as Bright and McGrail Banks, each with 10 genera. Photo samples from Stetson Bank had relatively low richness (8 genera), though not as low as Geyer Bank (4 genera) (Table 2). WFGB had the highest numbers of photos and ROV dives, and the largest area searched. Total area searched (> 50 m) on WFGB was three times the area searched on EFGB, but the numbers of photos and dives were more comparable (Table 2). The least effort was expended on Geyer and Bright Banks. Effort between banks was not as high as effort on McGrail and Stetson Banks, but area searched was comparable.

**Table 2. Generic richness and research effort by bank.** The number of putative genera occurring in photo samples from each bank are listed with the number of photo samples, the number of remotely operated vehicle dives, and the total area searched deeper than 50 m in square meters.

	Putative Genera	Sample Photos	ROV Dives	Area searched (sq m)
WFGB	20	2031	50	2,963,601
EFGB	17	1543	42	1,012,058
Between	11	322	8	274,668
McGrail	10	781	15	262,313
Bright	10	218	3	219,245
Stetson	8	424	11	209,104
Geyer	4	91	2	10,040

Generic richness was positively correlated with research effort in terms of area searched ( $p < 0.01$ ,  $r^2 = 0.71$ ), the number of photo samples ( $p < 0.01$ ,  $r^2 = 0.87$ ) and the number of ROV dives ( $p < 0.01$ ,  $r^2 = 0.86$ ). WFGB had the largest areal coverage, but fewer genera than expected, given the area searched. If WFGB were removed from the linear regression, the  $r^2$  increased to 0.87. This suggests diminishing returns in richness when the area searched was very large. Bright Bank and sites between banks had more genera than expected given the number of photos and number of dives. Photo samples from Bright Bank, WFGB, and McGrail Bank had highest Simpson's diversity, though genus richness for Bright and McGrail was moderate (Table 3).

Photos from Bright had moderate abundance, relative to others, but Simpson's evenness was high, and the ratio of genera to colonies was highest ( $10/400 = 0.25$ ). WFGB, EFGB, and sites between banks had highest abundance. WFGB ranked highly by Margalef D, but Bright Bank did not rank highly by the Margalef measure. Photo samples from McGrail, Stetson Bank, and sites between banks had moderate diversity by two measures, and Geyer Bank consistently ranked low. Few ROV dives occurred on Geyer Bank, and area searched was very low. Overall, deep octocorals were common on northwestern Gulf of Mexico banks, but the diversity of the assemblages varied by site.

**Table 3. Diversity, richness, and abundance by bank.** Study sites are ranked by two measures of diversity, Simpson's index (form  $1 - \lambda$ ) and Margalef's D. The number of colonies observed (N) is from all photo samples on each site. "Between" represents transects between EFGB & WFGB, all other categories are banks. WFGB = West Flower Garden Banks, EFGB = East Flower Garden Bank.

	Simpson Rank	Margalef Rank	Richness S	Colonies N	Evenness $E_{1/D}$	Simpson $1-\lambda$	Margalef d
Bright	1	5	10	400	0.56	0.82	1.20
WFGB	2	1	21	4510	0.23	0.79	2.60
McGrail	3	4	10	575	0.35	0.71	1.36
Stetson	4	6	7	108	0.41	0.65	1.08
Between	5	3	13	1213	0.19	0.59	1.46
EFGB	6	2	17	5203	0.13	0.55	1.97
Geyer	7	7	4	248	0.32	0.22	0.38

## DISCUSSION

A diverse assemblage of octocorals occurred between 55 – 120 m in the Flower Garden Banks region. We identified 24 unique species of octocorals, but recognize as many as 34 species maybe be present, primarily in the families Paramuriceidae and Ellisellidae. The species composition is consistent with earlier accounts from other banks (Rezak et al. 1985). Genera were grouped into two depth ranges: a group of three “shallow” genera (represented by *Swiftia* sp., *Diodogorgia nodulifera*, *Muricea pendula*) and a larger group of 11 “deep” genera. Genera were broadly distributed on surrounding banks, but also occurred on low-relief topography between banks. The only evidence of indigenous genera was *M. pendula*, which occurred numerous times on Stetson Bank (< 55 m) but only once on EFGB, and *Placogorgia tenuis*, which was photographed once on Southern Mound, a deep feature with 30 – 40 m relief at the base of WFGB.

Octocorals were most commonly observed in water 70 – 100 m deep. This was consistent with previous research (Rezak et al. 1985), which successfully characterized deep-water habitat on banks along the continental shelf in the region as sea fan habitat, even though the term “Antipatharian Zone” was invoked to describe the habitat (Bright & Pequegnaut 1974; Rezak et al. 1985, 1990). We improve upon the study with better taxonomic resolution. The original species list (Rezak et al. 1985) was drawn from other banks. Sample sizes were small, so depth ranges were given as maximum/minimum, whereas the photographic technique introduced here was sufficient to provide means and variance, and to discern between deep and shallow genera.

The term “Antipatharian Zone” needs revision, because the adjective is not entirely representative of the benthic assemblages characterizing the 50 – 120 m depth

zone. A rich assemblage of octocorals (24 species) shares this depth range with the antipatharians. Texts that introduced the terminology (Rezak et al. 1985, 1990) were cognizant of octocorals in this zone, because their species list identified more octocorals than antipatharians (Rezak et al. 1985, p. 226), and their charts of relative abundance indicated comparable numbers, albeit at slightly different depths (Rezak et al. 1985, p. 144). The term "Antipatharian Zone" was loosely applied based on the conspicuous abundance of *Stichopathes* at some sites, but octocoral genera can be confounded with Antipatharia. *Ellisella barbadensis* is an unbranched octocorallian sea whip sometimes mistaken for *Stichopathes*. *Hypnogorgia* and *Thesea* have white color morphs that may be confused with *Leiopathes*. The term "Deep Coral Zone" is more neutral, and more representative of the predominant fauna (Hickerson et al. 2008, Schmahl et al. 2008).

The known and potential richness of octocoral species in FGBNMS was increased by our study and shown to be higher than hard coral richness. However, taxonomic work remains incomplete for two reasons. Colonies in five genera remain to be identified, and species previously documented on the banks were not collected by the DFH surveys. Several genera that were collected have not been addressed in any comprehensive manner since the mid-1930s (e.g., *Caliacis*, *Hypnogorgia*, *Swiftia*, *Thesea*) or mid-1950s (e.g., *Placogorgia*). We successfully documented and mapped these taxa, so it should be possible to improve taxonomic resolution of Paramuriceidae by collecting a sufficient number of samples from FGBNMS for quantitative study. The taxonomy of octocorals in general is poorly resolved, and much in need of revision.

The effort devoted to identifying octocoral sample collections was a fraction of the effort devoted to performing ROV transects and collecting benthic photographs, but

together, the combination of taxonomy and image data provides a good characterization of the octocoral assemblage, relative frequency of occurrence, and predominant species. The high number of deep-water ROV transects on WFGB and EFGB (n = 106) will prove useful for hypothesis testing and maps of generic distributions. There were some weaknesses to the photographic technique. Problems associated with the image analysis were primarily related to species identification, but there were also issues with sample sizes, methodology, ROV tracking, and navigation that need improvement.

Black corals occurred within this depth range on FGBNMS so confusion may occur. The problem applied within the Octocorallia, too. *Muriceides hirta* and *Placogorgia tenuis* Verrill, 1883 are both large, yellow, reticulated sea fans. *Placogorgia* did not occur in the photo database because samples were collected late in 2003 with a work-class ROV better suited for sample collection than photo collection. These species may be confounded, though *Placogorgia* typically occurs with red and yellow morphotypes. So, the plots presented here most accurately depict the distribution of particular morphotypes, many of which are clear, e.g., *Thesea rubra* has distinctive biserial polyps, while other morphotypes are less distinctive, and may be one of two different species. The recommendation to other studies is to collect and identify as many colonies as possible, including the most diverse habitats, before transect work begins.

The most speciose taxa (*Ellisella* and *Nicella*) in this study were perhaps the most compromised by the taxonomic generalization because differences between species were obscured when binned to genus level. This may even help to answer the question of why *Ellisella* and *Nicella* were so abundant. Each genus had three species. Together they represented one quarter of all species collected, and 61% of colonies, but their biomass

may not be as high a proportion. Many are small colonies barely the size of a human hand. Their number likely represents an asexual means of reproduction or a recruitment episode. The largest colonies observed (*Muricea pendula*, *Placogorgia tenuis*) appeared to be concentrated, and the least abundant overall. The findings argue that gorgonians are broadly distributed in their depth range, but that optimal habitat may exist because colony size, richness, and frequency are high in discrete locales.

One of the primary questions to emerge from this analysis was: Why are the octocorals limited to deep-water on Flower Garden Banks? None of the caveats of the image analysis impinge on the fundamental observation that, in 8495 photos from 20 – 140 m, not a single octocoral was found shallower than 52 m. Support for a minimum depth threshold also lies in published ranges (Cairns & Bayer 2009b) for the species collected (see Table 1). Ten species have minimum depth values that fall within  $\pm 10$  m of the 55 m mark, so there appears to be a pattern.

Bayer (1961) noted that temperature was a limiting factor for Gorgonacea, invoking decreased temperature variability with depth as an explanation for the broad “homogenous” distribution of deep-water octocorals. Seasonally high water temperatures will induce octocoral mortality, and this has been demonstrated in the laboratory (Cary 1918). The 50 – 70 m depth range is consistent with the maximum seasonal depth of the mixing layer in the Flower Garden banks region (Rezak et al. 1985) and in the Caribbean (Wust 1964), where Ellisellidae and Paramurceidae occur (Bayer 1961).

Most coral reef biology to date has been engaged with a light-limited gradient of decreasing coral abundance with depth, but on FGBNMS the situation appears to be inverted, as dark-adapted azooxanthellate colonies reach upwards to the shallowest depth

limit of their tolerance. Under this scenario, the shallow group of octocorals (*Muricea pendula*, *Diodogorgia nodulifera*) would be expected to be most tolerant to temperature variability. *Swiftia* can grow very deep, so its presence is hard to reconcile. Further exploration of the regional oceanography will be required to resolve biotic and abiotic factors that influence gorgonian distribution in and around FGBNMS. However, if the depth of the surface layer does control the vertical distribution of deep octocorals, increased mortality or replacement of cold adapted octocoral species would be expected with the expansion of a warm surface layer in the West Atlantic.

We have discussed factors limiting cold-water Alcyonaria, but not factors limiting warm-water Alcyonaria. Plexauridae and Gorgoniidae are common in tropical settings of Florida and Mexico. Do the same characteristics that make Flower Gardens special (high coral cover, good health) also make the coral reef unique in regards to exclusion of shallow octocoral fauna? There is an inverse relationship between hard coral cover and gorgonian abundance (Kinzie 1970). The negative correlation could be maintained by recruitment limitation. FGBNMS is several hundred kilometers east of a convergence zone that may impinge upon westbound tropical coastal waters (Cochrane and Kelly 1986) dispersed seaward from Mexico, where shallow zooxanthellate gorgonians are common (Jordan-Dahlgren 2002), and quite dense in some places (Nelsen et al. 1988).

However, if shallow hermatypic zooxanthellate corals outcompete Alcyonaria, octocorals would be expected to occur on shallow banks with low coral cover. The nearest example to the west is the temperate Seven and One-half (7.5) Fathom Reef. The octocoral assemblage there is primarily *Leptogorgia* spp. So, depth appears to impose some limit to deep-water Alcyonacea even in the absence of competition. But, this is not

a good analogue to FGBNMS because 7.5 Fathom Reef is shallow, mid-shelf, and primarily tropical, though situated at nearly the same latitude as its temperate neighbors.

Low seasonal temperatures limit the distribution of some shallow tropical reef species in the northwest Gulf of Mexico (Rezak et al. 1985). Octocorals in the families Gorgoniidae and Plexauridae are part of the tropical reef community, and seasonally cold water could limit their presence in the northwestern Gulf (Bayer 1961). If the conjectures are true, octocoral assemblages in the northwestern Gulf develop between two seasonal temperature extremes, with winter minima limiting the presence of tropical species, and the summer maxima limiting upward distribution of deep-water species. The balance could be tenuous under a climate change regime.

Substrate, particle flux, and food availability are also important factors that limit octocoral distribution, and cannot be discounted (Bayer 1961, Peccini & MacDonald 2008). Our analyses confirm that depth is an important factor in FGBNMS, because we found significant differences in depth distribution between groups, and positive correlation ( $p < 0.01$ ,  $r^2 = 0.20$ ) between depth and richness on EFGB and WFGB. Depth is negatively correlated with temperature and exposure may, and this may explain the reduced abundance and diversity of the octocoral assemblage on Stetson Bank, because theoretically no parts of the bank (all  $< 55$  m) provide refuge from a dynamic seasonal climate. *Leptogorgia* spp. should be present because the genus occurs on the shelf and is reportedly well adapted to temperature and salinity flux (Bayer 1961).

Diversity and abundance were relatively high on some poorly studied features, so there is good justification for future research and exploration in the region. Different qualities were associated with different sites. WFGB and EFGB had high abundance and

richness, but EFGB had high dominance of *Ellisella* spp., hence low diversity. Bright and McGrail Banks ranked highly for diversity. Photo samples from Bright Bank and sites between banks were richer than expected (in the linear regression) given the effort devoted to these features. Sites between banks also had higher abundance than expected. Unexpected diversity and abundance could be the result of fortuitous diving in high quality octocoral habitat, result of some unidentified parameter, or, alternatively, result of locally optimal conditions.

The habitat documented between banks is worthy of particular note because the substrate was comprised of patch-reefs with relatively low-relief topography (2 - 10 m), presumably the remains of drowned reefs from the Pleistocene Era, a period of low sea-stand 100 – 120 m shallower than the modern shoreline (Rezak et al. 1985). Mississippi Pinnacles exhibit similar relief (Fig. 1). *Nicella* was among the most common benthic megafauna reported from Mississippi Pinnacles (Gittings et al. 1992). *Nicella* colonies were also abundant on the patch reefs, but the assemblage was relatively rich.

Low-relief habitat is difficult to detect in coarse bathymetry, so other habitats like these may not be obvious, or apparent. If drowned reef structures provide good habitat for mesophotic octocorals, the deep-coral habitat type might be fairly widespread on the shelf break in the northern Gulf, because banks are numerous, and patch reefs are a predominant deep-water habitat type surrounding EFGB and WFGB. This could be important because drowned reef habitats are nearly diverse biotically as the coral reefs (Rezak et al. 1985).

Future research using this database will seek to discern the nature of differences between photographs of octocoral assemblages on the banks. We report 24 species of

habitat forming octocorals, but recognize that as many as 34 species may occur in the region. Highest genus richness and genus accrual were on WFGB and EFGB. Photo samples from Bright Bank and McGrail Bank had unexpected diversity, so they should be targeted for study. Further investigation of sea fan habitat is warranted, because gorgonians appear to be broadly distributed in on high relief and low relief substrates deep-water. These octocoral assemblages are likely to provide food, shelter, and substrate to numerous associated species of fish and invertebrates.

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## CHAPTER THREE

### Comparison of Deep Octocoral Assemblages on Outer Continental Shelf Banks in the Northwestern Gulf of Mexico

by

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Running head: Comparison of octocoral assemblages

Key words: octocoral, deep-water, distribution, multivariate analysis, non-metric  
multidimensional scaling, banks, topographic features, Gulf of Mexico

**Comparison of Deep Octocoral Assemblages on Outer Continental  
Shelf Banks in the Northwestern Gulf of Mexico**

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**ABSTRACT:** Deep-water (> 50 m) octocorals occur on many of the 130 submerged pinnacles and banks that rise into the mesophotic zone (50 - 200 m) on the outer continental shelf (OCS) in the northwestern Gulf of Mexico. Octocorals in a database of 8495 geo-referenced seafloor images from 131 remotely operated vehicle transects on six OCS banks were identified to genus, and employed to: (1) test for differences between banks, and (2) to estimate the spatial scale of similarity for octocoral assemblages. Average abundance and richness per photo were compared using univariate tests. Composition of the octocoral assemblages was compared using multivariate tests. Hotspots for richness and abundance were identified using Moran's I and Getis-Ord  $G_i^*$  hotspot statistic on Flower Garden Banks. Genera were broadly distributed within and between banks. Average richness and abundance per photo, and the composition of the assemblages varied. Differences between banks were highly significant (ANOSIM,  $p < 0.001$ ), but were not related to depth. Similar depths on different banks within 50 km had different gorgonian assemblages (ANOSIM,  $p < 0.05$ ). Differences between sites may have been related to habitat heterogeneity or founder effects, while differences within sites were attributed to depth and topography. Hotspots for richness and abundance were evident on small raised features (30 – 40 m relief) at the base of East and West Flower Garden Banks.

## INTRODUCTION

Deep-water (> 50 m) octocoral species (soft corals, sea fans, gorgonians) occur in the Gulf of Mexico mesophotic zone (50 – 200 m), and create important structural habitat for associated species of fish and invertebrates. Deep octocorals are diverse and abundant, more so than shallow scleractinian corals (Cairns 2007a). They are highly adapted to cold and dark conditions. Their habitat is often neglected because it is “out of sight, and out of mind” (Roberts & Hirshfield 2004), although commercial fisheries and offshore oil and gas industries are moving increasingly into deep water (Rogers 1999, Roberts 2002). Marine protected areas around the world typically encompass deep water, but deep habitats within their boundaries are poorly explored relative to the shallow water domain. Mesophotic octocorals are often encountered upon and between abrupt topographies in deep water, but differences in nearby assemblages have not been studied.

Deep-water octocorals are broadly distributed on continental shelves, slopes, and seamounts throughout the world’s oceans where suitable substrate exists (Bayer 1956, Rogers et al. 2007). Warm temperatures are an important limiting factor (Cary 1918), but below the warm water layer (> 50 – 70 m) the geographic distribution of gorgonians could be interpreted as cosmopolitan, with a vertical range exceeding 5800 m (Cairns & Bayer 2009a). Bayer (1954) recognized depth strata and faunistic regions within the Gulf of Mexico, but he invoked a broadly homogenous West Atlantic octocoral assemblage in deep water, reaching as far as the Caribbean Antilles. Later analysis supported homogeneity (Giammona 1978). A broadly homogenous distribution creates a problem for deep conservation and management because it presents, essentially, a null hypothesis of no difference between sites, so priority setting and zoning becomes inherently difficult.

The null hypothesis of no difference between sites supplies a useful theoretical contrast to recent techniques seeking to classify and predict gorgonian habitat based upon well-known life-cycle parameters. For example, “suitable substrate” is generally interpreted as hard-bottom because planula larvae of octocorals and black corals do not settle on soft sediments, with few exceptions. Topographic relief is thought to be desirable because large coral colonies are commonly encountered on seamount peaks (Genin et al. 1986, DeVogeleare et al. 2005, Etnoyer 2008, Lundsten et al. 2009), in canyons (Mortensen & Buhl-Mortensen 2004, 2005), and on banks and mounds in the Gulf of Mexico (Rezak et al. 1985, 1990). High productivity and strong currents favor growth and reproduction since colonies are suspension feeders (Bayer 1961), orienting perpendicular to currents to maximize particle flux (Peccini & MacDonald 2008).

Developing a predictive habitat model should be straightforward with these few variables. Ecological Niche Factor Analysis was used to predict deep gorgonian habitat in two oceanic basins (Bryan & Metaxas 2007), but the study was overly broad, and as a consequence, bathymetry was coarse (4 km resolution), so the distribution model failed to identify known habitat (Etnoyer & Morgan 2007). Only a few studies compare deep-water gorgonian assemblages on similar features (Rezak et al. 1985, Gittings et al. 1992, Reed et al. 2005, 2006, Lundsten et al. 2009) at a local or regional scale (Deichmann 1936, Etnoyer & Morgan 2003, 2005), or even the basin scale in the Gulf of Mexico (e.g., Bayer 1954, Cairns & Bayer 2009b). Where statistical comparisons have been made, taxonomic resolution was coarse, at the scale of functional groups (Lundsten et al. 2009). There are exceptions (Giammona 1978, Watling & Auster 2005, Mortensen & Buhl-Mortensen 2004, 2005) but none to date for shelf banks in the Gulf of Mexico.

The outer continental shelf (OCS) banks in the northwestern Gulf of Mexico provide a good setting to test the null hypothesis of no difference between sites because 130 submerged pinnacles, banks, and topographic highs rise abruptly into the mesophotic zone (50 - 200 m) from a smooth, sediment-covered seafloor over 1000 km distance between the Mississippi River delta and the Mexican border (Parker & Curray 1956). Some of these features could be characterized as 'seamounts' because they are more than 100 m in relief (Pitcher et al. 2007), but the features are technically salt diapirs, referred to as banks (Rezak et al. 1985). The concentration of features along the shelf break provides a good opportunity to study gorgonian distribution because: (1) feature density is relatively high, (2) feature size is relatively small, < 5 km radius, and (3) sampling coverage is good, so sample sizes are large, and statistical power is relatively high.

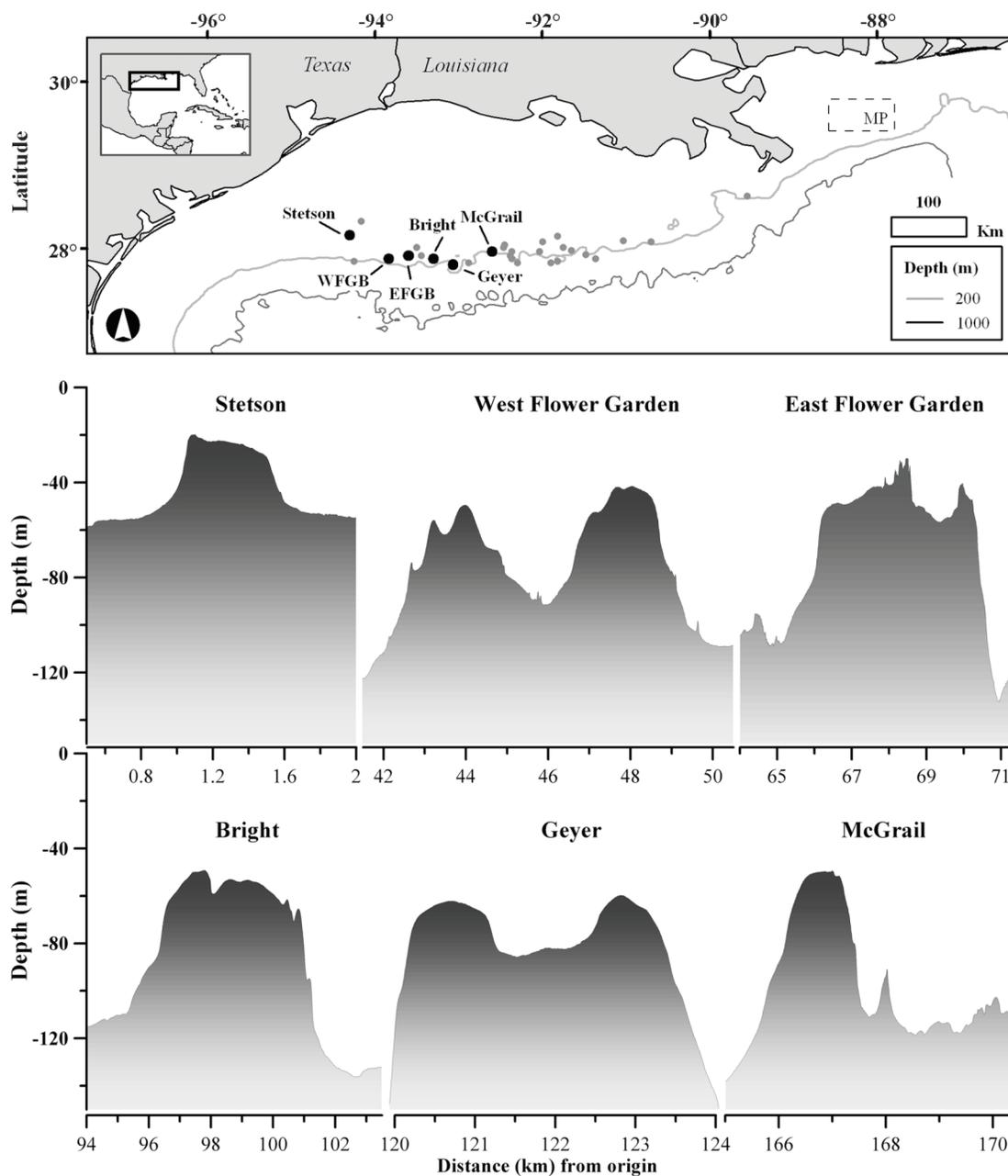
The questions addressed in this manuscript are not unlike the investigations of contemporary researchers in the Census of Marine Life on Seamounts (Pitcher 2007). The scale of analysis differs substantially because the OCS banks are small (50 - 200 m relief) and close together. Nevertheless, OCS banks serve as a good regional case study of benthic assemblages on raised topography in the Gulf of Mexico. Specifically, we ask: Does the composition of octocoral assemblages vary between features? What is the spatial scale of similarity between features? Are there "hotspots" for richness and abundance? We use a database of 8495 geo-referenced seafloor images (Chapter 2) drawn from 131 remotely operated vehicle (ROV) transects on six submerged banks (50 - 200 m relief) within a 100 km radius to examine the scale of similarity for gorgonian assemblages, and to test the null hypothesis of no difference in gorgonian distributions between banks in the Gulf of Mexico.

## MATERIALS AND METHODS

A database of 8495 geo-referenced seafloor images from a series of Deep Fish Habitat (DFH) expeditions 2001-2005 was analyzed. Images were from transects conducted using the Phantom S2 ROV National Undersea Research Center/University of North Carolina at Wilmington. The database encompassed surveys of three submerged banks in Flower Garden Banks National Marine Sanctuary (FGBNMS): Stetson Bank, East Flower Garden Bank (EFGB), and West Flower Garden Bank (WFGB), plus three other major topographic features along the outer continental shelf break in northwestern Gulf of Mexico- Bright, McGrail, and Geyer Banks. Mud volcanoes and sites between EFGB and WFGB were grouped into a single category, hereafter “sites between”.

A location map is provided in Figure 1 with profiles of relief for each of the six submerged banks. The banks range from 50 m (Stetson Bank) to 200 m in relief (Geyer Bank), positioned along a 200 km interval of the OCS break in the northwest Gulf of Mexico. Profiles of relief were generated using ET GeoWizards 9.7 tools in ArcGIS 9.2 (ESRI 2008) at 10 m step intervals along identical aspect cross-sections over high-resolution (4 m) multibeam bathymetry for each of the study features (Gardner et al. 1998, Gardner & Beaudoin 2005). To minimize horizontal distortion, coordinates for each depth value were derived using the Euclidian distance formula from a common point on the shelf break 500 km west of the westernmost feature, Stetson Bank. Stetson Bank is classified as a mid-shelf bank. The others are OCS banks along the shelf break.

Photos were collected with a Scorpio 3.2 megapixel digital camera (Insite Pacific) mounted at an oblique angle on the Phantom S2 ROV. The photo-documentation method was exploratory. Photos were non-random, chosen to represent conspicuous epifauna and



**Figure 1. Location of study sites and depth profiles for six banks.** Outer continental shelf banks in the northwestern Gulf of Mexico (top panel, black dots) are shown with vertical profiles (bottom panel). Labels indicate study sites, letters indicate features discussed in the manuscript. WFGB = West Flower Garden Bank, EFGB = East Flower Garden Bank, MP = Mississippi Pinnacles.

to characterize benthic habitat in a qualitative manner. The octocoral study we present must be considered a meta-analysis, because the original intention of the research was to characterize deep fish habitat, not to compare octocoral assemblages between features. The analysis was justified because the data represent an unprecedented research effort (48 days of mapping, 87 days of ROV and submersible work) within a poorly known deep-water habitat. Efforts were made to compensate for bias and to introduce independence, but these cannot eliminate bias, so caution must be exercised in the interpretation. The photo data were treated as random and independent to justify the analyses.

Video data was also collected, but frame grabs from video data were not employed in this analysis. Future treatments of that information will be forthcoming. This manuscript seeks to characterize octocoral habitat, so taxonomic resolution was the highest priority. Standard definition video frame grabs would have introduced taxonomic uncertainty, because high-resolution photo images were necessary to distinguish between genera. The primary bias in the documentation methodology was that soft bottom habitats were not well represented, but most octocorals are not well suited to soft substrate, so the bias was considered acceptable.

A subset of 6504 images deeper than 50 m was selected from the 8495 images available. The justification for the subset is that no octocorals occurred shallower than 52 m (Chapter 2), so shallow depths were not considered octocoral habitat *per se*. Only 1/5th of 6504 images depicted gorgonians. Null data were available from both shallow and deep water. Quality control procedures removed 1096 duplicate and replicate images from the subset of 6504. Replicate images were defined as different photo extents of the same colonies (changes in the photo angle or zoom). The resulting data for analysis

**Table 1. Presence and absence of octocoral genera in the northwestern Gulf.** The tables shows presence and absence of octocoral genera on northwestern Gulf of Mexico banks surveyed between 2001 and 2005. Study sites (banks) are across the top. Genera are in italics, codes for unidentified genera are in plain text. WFGB = West Flower Garden Bank, EFGB = East Flower Garden Bank.

Octocoral genera	ROV Dive Location						
	Stetson	WFGB	Between WFGB & EFGB	EFGB	Bright	Geyer	McGrail
<i>Ellisella</i>	X	X	X	X	X	X	X
<i>Nicella</i>	X	X	X	X	X		X
<i>Hypnorgia</i>	X	X	X	X	X	X	X
<i>Scleracis</i>	X	X	X	X	X		X
<i>Caliacis</i>	X	X		X	X		X
<i>Chironepthya</i>		X	X	X	X		X
<i>Bebryce</i>		X		X	X		X
<i>Thesea</i>		X		X	X		
DFH8_16A		X	X	X		X	
<i>Callogorgia</i>		X	X		X		X
<i>Muricea</i>	X			X			
<i>Muriceides</i>		X	X				
<i>Swiftia</i>	X	X		X		X	X
<i>Diodogorgia</i>		X		X			
Unidentified	X	X	X	X			X
DFH11_12A		X	X	X			
<i>Thelogorgia</i>		X	X	X	X		
G5		X		X			
G9		X		X			
<i>Leptogorgia</i>		X					
G2		X					

consisted of 5408 images, of which 1/4 depicted octacorals. Research effort varied on features (Table 1). WFGB and EFGB had the highest spatial coverage.

The 50 m minimum depth value was rounded from 52 m to account for discrepancies between actual, observed, and interpolated depths. Depths observed on the video overlay from the ROV differed from actual depth by 1- 2 m. Depth values were not always recorded due to technical malfunction or operator error, so blank values were augmented by multibeam depth values for each photo location. Multibeam depth values

were within 5 m of observed depth values 70% of the time, and within 10 m 90% of the time. Depth accuracy was less critical than large sample sizes for this investigation, so multibeam depths were adopted and applied. Comparisons are based primarily upon assemblage characteristics, i.e. the number of colonies per genus. The only comparison that employs depth is a comparison of images from similar depths (50 - 60 m).

Voucher collections were made to identify octocoral colonies using Scanning electron microscopy (SEM) of diagnostic sclerite features with consultation from established octocoral authorities at Smithsonian National Museum of Natural History. Identifications were applied to images post-hoc. Each of 8495 photo samples in the overall DFH photographic geo-database included fields for a unique identifier (ID), cruise number, dive number, photo name, latitude, longitude, observed (ROV) depth, and multibeam depth, followed by a list of 21 octocoral genera with values for the number of colonies per photo (0 – 90). The data were prevalence, not incidence, because several colonies of different genera could occur within any given image (Fig. 2).

To help compensate for bias, random samples were selected from each location for non-metric multidimensional scaling (MDS) analyses between banks ( $n = 90$ ) and between like depths (for each site,  $n = 125$ ). Random images were selected using the first 90 (or 125) entries in a random sequence (<http://www.random.org/sequences/>) bounded by sample size at each study site. Randomly selected images were used for univariate (richness and abundance per photo) and multivariate (abundance values for 21 genera) comparisons of photo samples between banks.

The primary operational taxonomic unit used in the database was octocoral genus. However, some morphotypes were unidentified. Rare unidentified morphotypes were



**Figure 2. An example image from the geo-referenced photo database.** This example image is one of 5408 geo-referenced photographs deeper than 50 m. It depicts a rich octocoral assemblage comprised of *Bebryce*, *Chironephyta*, *Callogorgia*, *Ellisella*, *Nicella*, and *Scleracis* on McGrail Bank, 94 m deep.

classified as “unidentified”, while common unidentified morphotypes were assigned a code (e.g. G5). Coded morphotypes comprising less than one-tenth of one percent of colonies (G5 - G13) in images  $\geq 50$  m were deleted from analyses. The threshold was low (0.1 %) because some rare colonies were important components of certain banks, but coded morphotypes represented a taxonomic uncertainty that should be removed. The resulting dataset retained 15 true genera, two coded morphotypes “DFH8\_16A” and “DFH811\_12A”, and one group of unidentified octocorals “Unid.” for 18 total variables.

The subsampling procedure for like depths further reduced the variables to 13 true genera and one morphotype “DFH8-11A”, hereafter referred to simply as genera.

Univariate and multivariate techniques were used to compare and contrast photographs of gorgonian assemblages between sites. Photos were the sample units and banks were the treatments. Variables for generic richness and total abundance were compared using the non-parametric Kruskal-Wallis statistic with a modified Scheffe’s post-hoc test (Day & Quinn 1989). Abundance data for octocorals  $\geq 50$  m (5408 images, 10,819 colonies) were highly positively skewed toward zero (73% of values) and one (9% of values). No transformation fit the data to a normal distribution, so non-parametric analyses were necessary. The null hypothesis of the same distribution was tested against the alternative that values were higher in other populations using Kruskal-Wallis (Neal 2009). Scheffe’s post-hoc test is parametric, so it was not ideally suited to the data, but the test is applicable to unequal sample sizes, highly discriminatory, and conservative, with low chance of Type I error (Day & Quinn 1989), so the approach was useful.

Multivariate data from the random subset of images were analyzed using Analysis of Similarity (ANOSIM) Global  $R$  statistic to detect and identify significant differences in photo samples from each bank (Clarke & Green 1988). ANOSIM  $R$  is a non-parametric permutation procedure in the software PRIMER 6.1 (Clarke & Gorley 2006). ANOSIM was used on an underlying Bray-Curtis similarity matrix to rank similarity, and calculate a global  $R$  statistic from the fraction of the difference between average rank similarity *within* groups and average rank similarity *between* groups over a function of the number of samples. The resulting  $R$ -value ranges between 0 and 1, indicating the degree of

discrimination between sites. A small value could be statistically significant if there were many replicates at each site (Clarke & Green 1988), as was the case here.

The rationale of the ANOSIM permutation test is that there should be no effect on the average value of  $R$  when sites associated with samples are arbitrarily rearranged if there is no difference between sites. Site factors are reshuffled in subsequent iterations to generate a null distribution of  $R$ . The number of permutations is a function of the number of sites and samples. The significance of  $R$  is calculated by referring the observed value of  $R$  to the spread of values generated by the random rearrangements. If the observed value is unlikely to come from the null distribution, the null hypothesis can be rejected (Clarke & Warwick 2001).

Pair-wise tests and other subroutines were also performed using PRIMER 6.1. Pairs of sites were extracted, re-ranked, and the ANOSIM test procedure repeated. If less than 5% of the values in the null distribution for  $R$  were equal to or larger than the observed  $R$ , then the null hypothesis was rejected at the level  $p < 0.05$ . Interpretation is important, because 1 in 20 comparisons will incorrectly reject a true null (Type I error) at the level of  $p < 0.05$ . Caution must be exercised if the stress value of the ordination is  $>> 0.10$ . Stress values  $< 0.20$  should be crosschecked against other techniques, such as hierarchical clustering analysis (Clarke & Warwick 2001).

In this study, the ANOSIM statistic was used for the purposes of estimating whether: (1) gorgonian assemblages were significantly different between sites ( $n = 630$ ); (2) octocoral occurrences in shallow images (50 - 60 m) were significantly different on Stetson, McGrail, EFGB, and WFGB ( $n = 500$ ); (3) mean abundance of octocoral genera was significantly different between sites ( $n = 28$ , three subset means and 1 overall mean

for each of 7 sites); and, (4) whether pair-wise comparisons were significantly different in each of the three cases above. A non-metric multi-dimensional scaling (MDS) plot is shown twice, once to illustrate similarities and differences in overall means ( $n = 90$ ) and subset means ( $n = 30$ ) for images from each study site; and secondly, to compare the MDS plot for 630 photo-samples to the MDS plot for 28 means.

The ordination of 630 data points was difficult to interpret, even when separation between groups was significant. For example, sites with high richness and abundance and sites with low richness and abundance had images with no gorgonians, so these images would be 100% similar, and plot the same. The reason for plotting subset means was to reduce the number points in the plot, and to understand the variance in means for each site. The intended purpose of the MDS plot was to illustrate patterns, while the intended purpose of the ANOSIM  $R$  tests was to test for significance of differences underlying the patterns. A significant difference was defined as  $p < 0.05$  and a highly significant difference is  $p < 0.001$  for the purposes of this manuscript.

Abundance values were zero-adjusted (Clarke et al. 2006) and square root transformed to down weight the importance of abundant genera as a pre-treatment to the Bray-Curtis similarity procedure for comparisons between sites. No transformation or adjustment was applied to the comparison of means. The zero adjustment consisted of a dummy variable with a value of one for all photo-samples. In this way, the denominator in the Bray-Curtis equation was never zero, so values were not “undefined”. The key assumption for the procedure was that all images devoid of octocorals were null for the same reason. This was satisfactory because images  $< 50$  m depth were excluded, so the

one factor known to limit octocoral distribution on the banks (depth) was eliminated. If we compared soft-bottom to hard-bottom, the assumption might be less satisfactory.

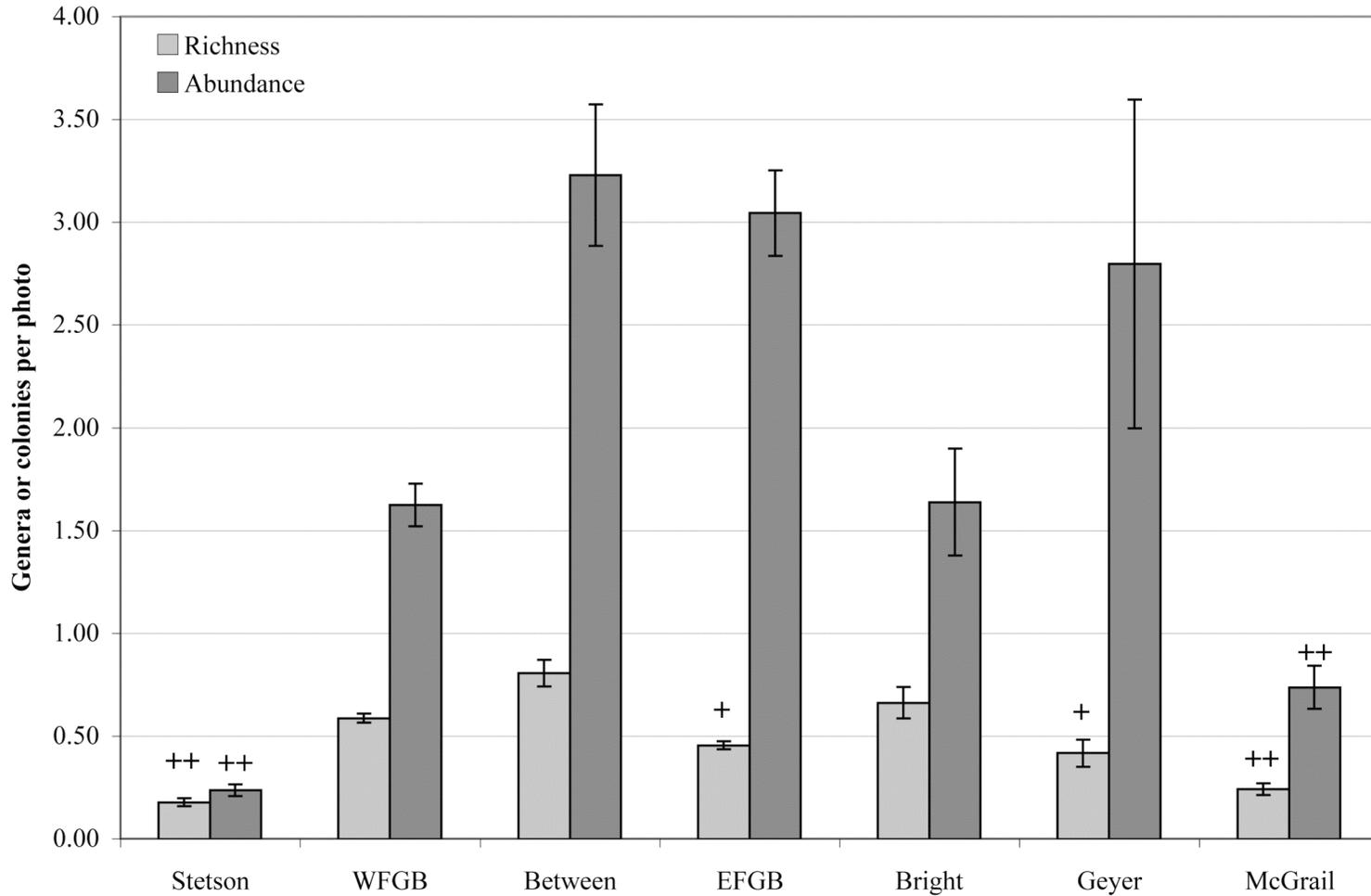
Pair-wise subroutines conducted in PRIMER 6.1 to discriminate the genera driving differences between banks were applied singly using bubble plots, and in combination using the BEST and SIMPER procedures. Bubble plots represent the values of each variable by scaling the size of the bubble to the value, superimposed on the ordination plot for the corresponding samples (Field et al. 1982). BEST identifies combinations of variables that best explain community patterns, using the BIO-ENV algorithm (Clarke & Ainsworth 1993, Clarke 1993). The maximum number of variables was set to five. The Similarity Percentage Breakdown (SIMPER) procedure identified genera discriminating between any two sites in the MDS ordination.

Comparisons of octocoral distribution within sites were limited to the two most intensely sampled banks (WFGB & EFGB) using Spatial Analyst extension of ArcGIS 9.2 (ESRI, 2008). Moran's I index (Moran 1950) measured spatial auto-correlation using feature location (coordinates) and feature values (richness or abundance) to calculate an index value and a Z score to test the hypothesis of no spatial clustering. The Getis-Ord  $G_i^*$  (Ord & Getis 1995) hotspot statistic was used to compare generic richness and octocoral abundance to the mean value for all images within a specified threshold distance. We used an inverse distance weighted algorithm with Euclidian distance measure and a threshold distances from 0.1 – 2.0 km. The settings stipulated that the impact of one data point on another decreased with distance, that this distance was a straight line, and that features outside 0.1 – 2.0 km threshold distance were ignored.

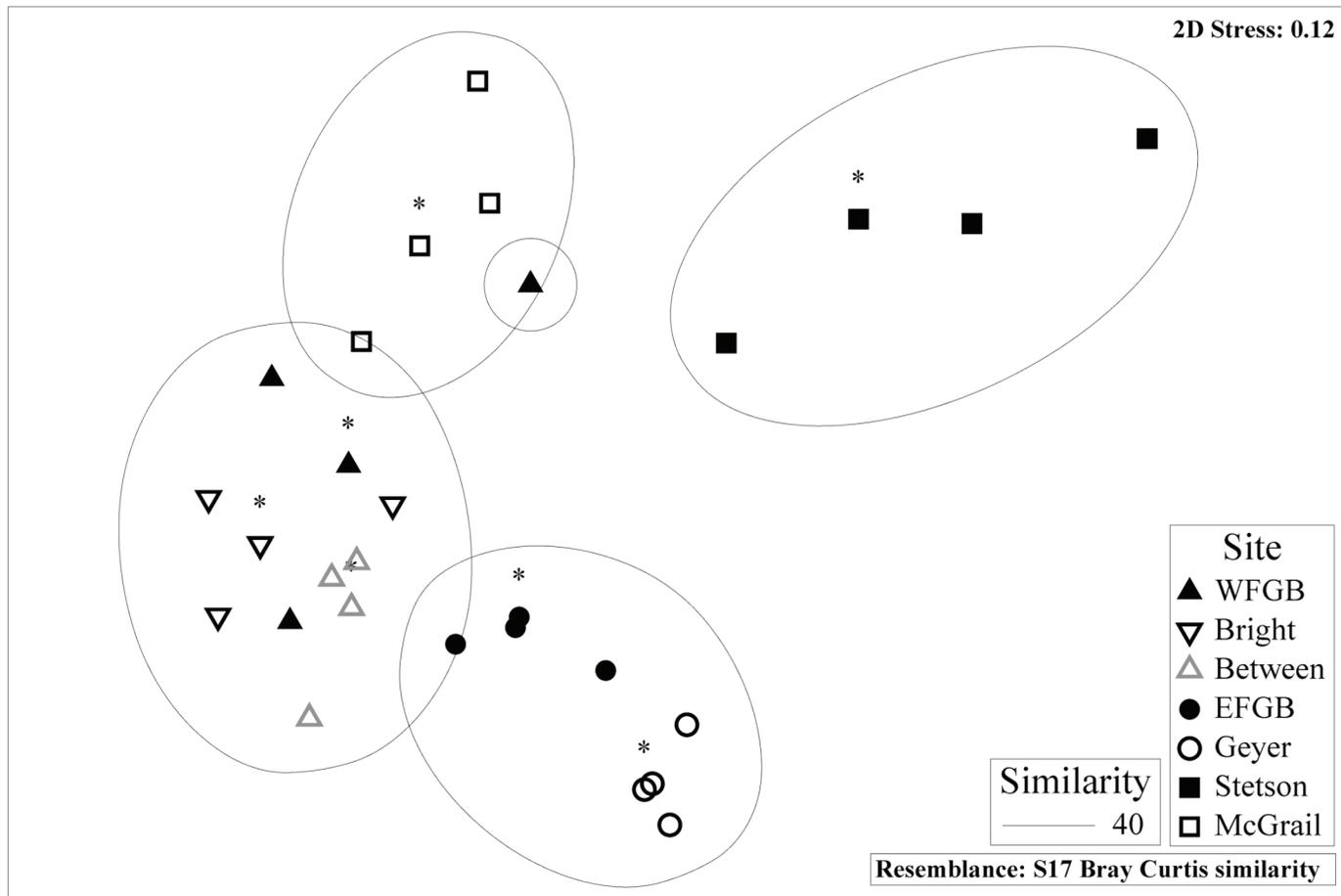
Getis-Ord  $G_i^*$  hotspot statistic was used to identify clusters of points with values higher in magnitude than might be expected by chance alone. Positive  $Z$ -values represented the number of standard deviations above the mean richness (0.5 for all photos > 50 m, 1.75 for all images with corals) or mean abundance (1.85 and 7.0, respectively). For 95% confidence that richness or abundance values were higher in magnitude than would be expected by chance alone, the Getis-Ord  $G_i^*$   $Z$  value would have to be greater than 1.96, for 99% confidence the values would be  $> 3$ . These  $Z$  values were mapped in concert with observed richness and abundance values on EFGB and WFGB in ArcGIS 9.2 using the UTM Zone 15 projection with WGS84 datum, consistent with the 4 m resolution bathymetry data.

## RESULTS

Octocorals were found deeper than 50 m on all six banks (EFGB, WFGB, Stetson Bank, McGrail, Bright, Geyer) as well as sites between (Table 1). There were highly significant differences in average generic richness (Kruskal-Wallis,  $df = 6$ ,  $p < 0.001$ ), and average abundance per photo (Kruskal-Wallis,  $df = 6$ ,  $p < 0.001$ ) (Fig. 3). The composition of the deep gorgonian assemblage also varied between sites (ANOSIM,  $p < 0.001$ ). Photo samples from seven sites fell into four distinct groups with approximately 40% similarity (Fig. 4). Stetson Bank and McGrail Bank were independently grouped. EFGB and Geyer Bank were similar. WFGB, Bright Bank, and sites between constituted a fourth group. Differences were also evident within sites. Values for richness and abundance on EFGB and WFGB were highly spatially auto-correlated at scales from 0.1-2 km (Moran's  $I$ ,  $p < 0.001$ ) and hotspots were evident.



**Figure 3. Average richness and abundance of photo samples by site.** Average richness per photo (light gray bars) and average abundance per photo (dark gray bars) are plotted with one standard error for each study site. A single plus (+) indicates values significantly different from 3 sites, double plus signs (++) indicate values significantly different from 5 sites (Scheffe's post-hoc test,  $df = 6$ ,  $p < 0.05$ ).

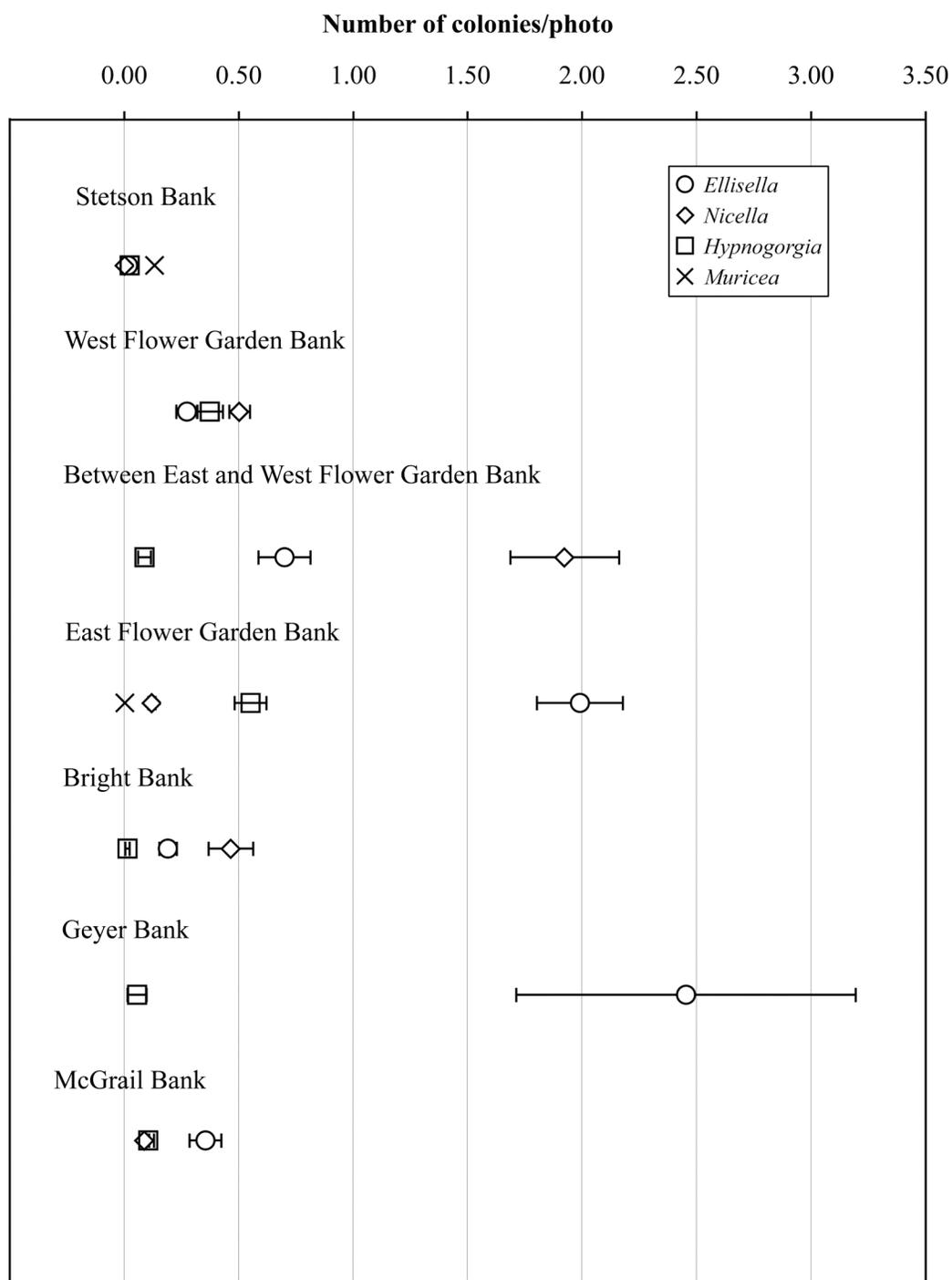


**Figure 4. Ordination of photo sub-samples by site.** A non-metric dimensional scaling (MDS) plot of Bray-Curtis dissimilarity values for mean octocoral abundance per genus ( $n=14$ ) for : (1) all randomly selected photos ( $n=90$ , symbolized by an asterisk) and (2) random subsamples ( $n=33$ , with no asterisks). The technique illustrates mean and variance, grouping seven sites into four significantly different assemblages (ANOSIM,  $p < 0.001$ ) with 40% similarity.

The distribution of octocoral genera varied from cosmopolitan (defined here as a genus occurring on all sites) to relatively rare, or indigenous (defined here as a genus occurring on one or two sites). There was a significant difference in abundance between genera (Kruskal-Wallis,  $df = 17$ ,  $p < 0.001$ ). *Ellisella*, *Nicella*, and *Hypnogorgia* were most cosmopolitan and most abundant (0.8 to 0.3 colonies per photo). Abundant genera occurred at every site, with one exception. *Nicella* was not documented on Geyer Bank. Presence and absence of octocoral genera are reported for each bank in Table 1.

*Callogorgia*, *Muricea*, *Thelogorgia*, *Leptogorgia*, and *Swiftia* were relatively uncommon ( $\sim 0.01$  colonies per photo). *Leptogorgia*, *Muricea*, and *Diodogorgia* were rare, because they occurred at one site, or at most, two sites. *Muricea* was relatively abundant on Stetson Bank (Fig. 5). *Muricea* occurred only once on EFGB. *Leptogorgia* was photographed twice on WFGB with high abundance (25 & 30 colonies). *Diodogorgia* and unidentified morphotypes G2, G5, G8, and G9 occurred only on EFGB and WFGB. Maps of abundance and distribution of each genus are provided for the banks that comprise FGBNMS- EFGB, WFGB, and Stetson Bank (Appendix 3).

Highly significant differences in gorgonian assemblages (18 octocoral genera) occurred between sites (Bray-Curtis dissimilarity matrix of root-transformed abundance values, ANOSIM,  $p < 0.001$ ). Pair-wise tests for differences between banks were illustrated in the clusters circled by 40 percent similarity contours in the MDS plot of mean abundance values (Fig. 3). Overall means for each site ( $n = 90$ ) were plotted with subset means ( $n = 33$ ) to illustrate variance, and to facilitate graphic representation of similarity clusters.



**Figure 5. Average abundance of common octocoral genera by site.** Mean octocoral abundance per photo is plotted by genus for each of six submerged banks in the Gulf of Mexico. *Ellisella*, *Nicella*, *Hypnogorgia*, *Caliacis* and *Muricea* explain 92% of the variance among sites. *Muricea* is typical of Stetson Bank. Other genera are more abundant and more cosmopolitan. *Caliacis* is not plotted.

The significant differences in the ANOSIM results for the ordination of means ( $n = 28$ ) were similar to results for the ordination of samples ( $n = 630$ ). Raw, untransformed values were used in the MDS for means. Stress was low (0.12, Fig. 4), corresponding to a good ordination with slight prospect of a misleading representation (Clarke & Warwick, 2001). Differences in means were highly significant (ANOSIM,  $p < 0.001$ ). The MDS for all samples, root transformed, had slightly lower stress (0.10, Appendix 4). Differences between photo samples were also highly significant (ANOSIM,  $p < 0.001$ ). Mean generic abundance values were not significantly different between EFGB and Geyer.

The interpretation of the axes in the ordination plots was based upon “bubble plot” rendering of all generic variables, and values for richness and abundance. A gradient from abundance of rare species (*Leptogorgia*, *Muricea*) to abundance of cosmopolitan species (*Bebryce*, *Nicella*) explained part of the separation (one axis) in the MDS plot for all samples (Appendix 4). High abundance of *Hypnogorgia* (75 colonies) and *Ellisella* (90 colonies) discriminated between samples on the second axis. Highest values for these two genera occupied opposite extremes. The axes of the MDS plot for means (Fig. 4) were more straightforward. The central aggregation of points represents genera typical of WFGB, Bright Bank, and sites between. Radiations from the center represent the abundance of genera that typify those sites- *Muricea* for Stetson Bank, *Ellisella* and DFH8\_16A on EFGB and Geyer, and the low abundance of *Scleracis*, *Callogorgia*, *Caliacis* and *Bebryce* that characterize McGrail Bank.

Average richness and abundance *per photo* did not explain the axes of ordination clusters, though there were highly significant differences in average richness and abundance per photo between banks (Kruskal-Wallis,  $p < 0.001$ , Fig. 3). Images from

Stetson Bank had significantly lower average richness (0.18 genera/photo) than images from all other sites except Geyer and McGrail (Scheffe's test for richness,  $p < 0.05$ , Appendix 5). Highest richness per image was between sites (0.81 genera per photo), though not significantly different than Bright. WFGB and Bright had high intermediate richness (0.59, 0.66 genera per photo). EFGB and Geyer Bank had low intermediate richness (0.42, 0.45 genera per photo). Groups were consistent with the clusters in the MDS ordination for means.

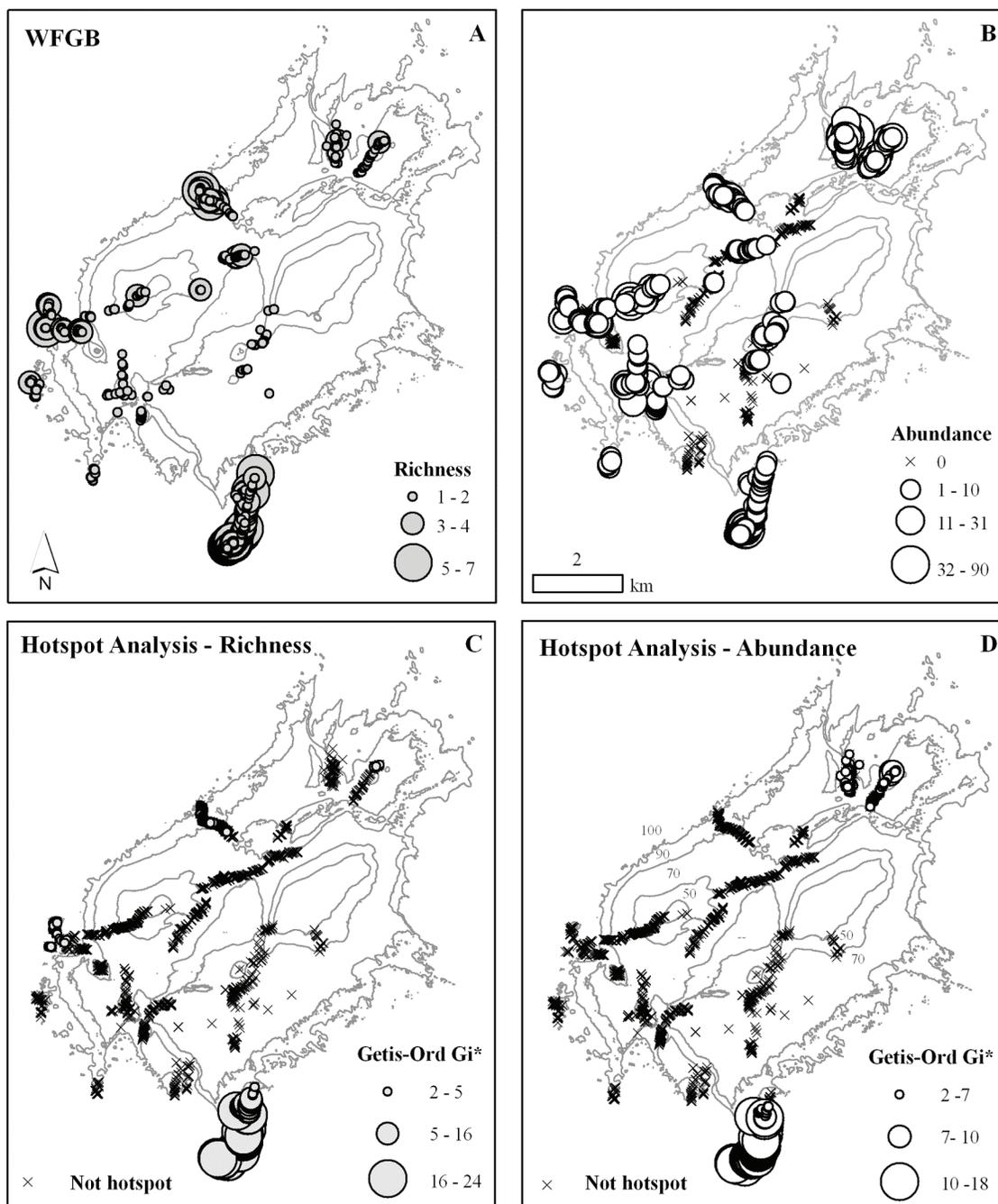
Highest average abundance per photo occurred on EFGB and sites between (3.04 & 3.23 colonies per photo, respectively). Lowest average abundance per photo was on McGrail Bank (0.25 colonies per image). Average abundance per photo was not significantly different on Stetson and McGrail, between sites and EFGB, or EFGB and Geyer (Scheffe's test for abundance,  $p > 0.05$ , Appendix 5). These groups were consistent with the clusters in the MDS plot for means (Fig. 3). Thus, differences in assemblages between banks were robust across methods.

The differences between banks were not entirely related to depth, because photos ( $n = 125$ ) from the same depth range (50 - 60 m) on sites with 'shallow' octocorals (Stetson, WFGB, EFGB, Bright, McGrail) were all significantly different (ANOSIM,  $p < 0.05$ ), except in two cases. Photo samples of assemblages on EFGB and WFGB were not significantly different, and photo samples of Bright and McGrail were not significantly different. Large sample sizes were prerequisite to these results. Low sample sizes ( $n = 50$ ) did not yield significant differences in pair-wise comparisons. Bright and McGrail had no octocorals 50 – 60 m, so this would explain their high degree of similarity (100%).

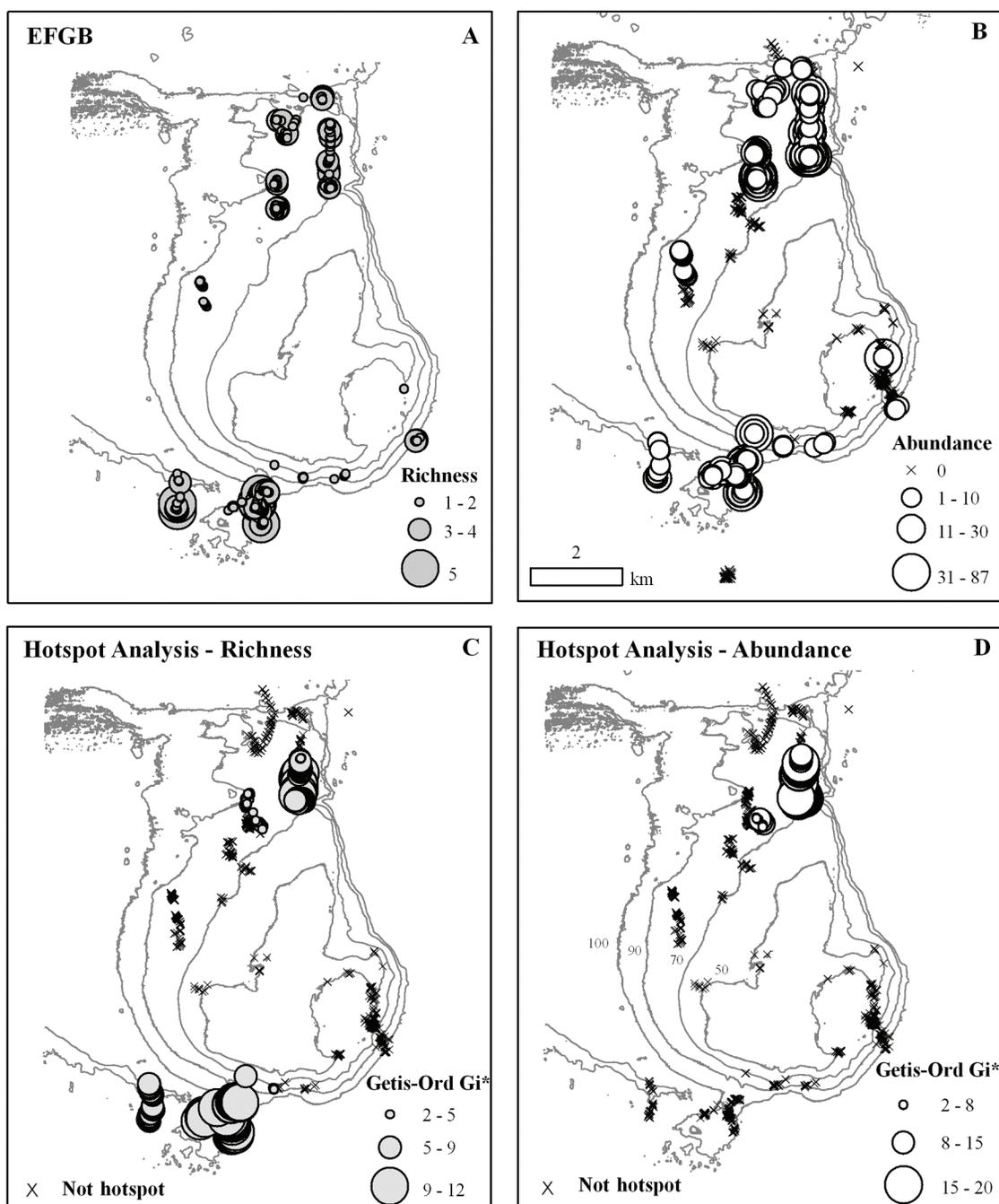
The three most abundant genera in the region- *Ellisella*, *Nicella*, and *Hypnogorgia* (Appendix 6) ranked highest in the BEST analysis of variables driving differences between banks. *Muricea* and *Caliacis* ranked second highest. Together, the five genera explained 92% of the variance between sites, and accounted for an average of 76% ( $\pm$  4.65%) of the cumulative dissimilarity between any two sites in the SIMPER analysis. *Swiftia* and *Scleracis* were also important discriminators.

The simplest representation of the differences in composition for the octocoral assemblages on each site was a plot of the average abundance of the three highest ranked discriminators, plus *Muricea* (Fig. 5). *Caliacis* added no new information to the plot following these four genera. Geyer and EFGB were characterized by a relatively high abundance of *Ellisella*, while Bright, WFGB, and sites between were characterized by a relatively high abundance of *Nicella*. Stetson Bank was unique in that it is characterized by relatively high abundance of *Muricea*, absent from all other sites except EFGB. McGrail Bank had low overall abundance for all three genera. These values were consistent with the representation and interpretation of the MDS plot for means (Fig. 4).

Within site comparisons were limited to EFGB and WFGB, because coverage and effort was highest at these sights. Generic richness and abundance values were significantly auto-correlated (Moran's I index of spatial autocorrelation,  $p < 0.01$ ). Changes in the distance threshold (100 m – 2,000 m) had no effect on the significance level of these results. Deep hotspots for richness and abundance were present on WFGB (Fig. 6) and EFGB (Fig. 7) (Getis-Ord  $G_i^*$ ,  $p < 0.05$ ). Values were significantly higher than average on mound features directly to the north and south of each site, and upon other small mounds (10 - 50 m) at the base of the banks. Mean richness and abundance



**Figure 6. Maps of hotspots for richness and abundance on Flower Garden Banks.** Richness (A) and abundance (B) of octocorals are overlaid on West Flower Garden Bank bathymetry (Gardner et al. 1998) with hotspot statistics for each of these parameters (bottom panels – C, D). Getis-Ord  $G_i^*$  hotspot values (Ord & Getis 1995) indicate the number of standard deviations above the mean within a fixed search radius of 1000 m. Images with no octocorals are indicated by an “x”.



**Figure 7. Maps of hotspots for richness and abundance on Flower Garden Banks.** Richness (A) and abundance (B) of octocorals are overlaid on East Flower Garden Bank bathymetry (Gardner et al. 1998) with hotspot statistics for each of these parameters (bottom panels – C, D). Getis-Ord  $G_i^*$  hotspot values (Ord & Getis 1995) indicate the number of standard deviations above the mean within a fixed search radius of 1000 m. Images with no octocorals are indicated by an “x”.

on WFGB was 0.59 genera/photo and 1.62 colonies/ photo. Mean richness and abundance on EFGB was 0.45 genera/photo and 3 colonies/photo (Fig. 3). WFGB had more hotpots than EFGB, and they were more broadly distributed. Hotspots for richness and abundance did not always overlap.

In summary, the octocoral assemblages on OCS banks were highly significantly different and groups were robust across different statistical techniques. Differences between banks could not be explained by effort, because a balanced, random sample of images was used to discriminate between sites. Differences did not appear to be related to peak height, depth, or distance between banks because similar depths on features within 100 km had different gorgonian assemblages (ANOSIM,  $p < 0.05$ ). Differences between average richness and abundance were very highly significant (Kruskal-Wallis,  $p < 0.001$ ). The null hypothesis of no difference between sites is rejected with confidence. Octocoral genera were broadly distributed, but composition varied between and within sites, and hotspots for richness and abundance were evident on deep mound topography at the base of EFGB and WFGB.

## **DISCUSSION**

Deep-water octocorals were broadly distributed on outer continental shelf banks in the mesophotic zone of the northwestern Gulf of Mexico (Rezak et al. 1985); octocorals occurred on all banks and all sites between banks below a threshold depth of 50 m. The broad distribution of octocorals does not imply that the gorgonian assemblage at each site was the same. Overall richness ranged from 7 genera (Stetson Bank) to 14 genera (WFGB), excluding unidentified genera. The abundance and predominance of known genera varied substantially on features less than 30 km apart. For example, EFGB

had two colonies of *Ellisella* and 0.5 colonies of *Hypnogorgia* on average per photo, while *Nicella* was relatively rare (Fig 2). Bright Bank had 0.45 colonies of *Nicella* and 0.25 colonies of *Ellisella* per photo, while *Hypnogorgia* was relatively depauperate. *Muricea* occurred on Stetson Bank in moderate abundance, but *Muricea* was rare on EFGB, and absent elsewhere.

The study represents a novel interpretation of deep coral assemblages in the Gulf of Mexico because we used a suite of univariate and multivariate statistical techniques with mild transformations applied to generic level abundance values to identify highly significant differences. Other studies characterizing topographic highs in the northwest Gulf of Mexico placed Alcyonaria in a functional group (Rezak et al. 1985) or limited discrimination to the most abundant genera (Gittings et al. 1992). A study comparing benthic assemblages on seamount features in the Northeast Pacific (Lundsten et al. 2009) found octocorals were cosmopolitan. No differences were evident, but octocorals were grouped generally (Alcyonacea and Gorgonacea). The approach may be justified, because average abundance of colonies will discern banks, but nuances related to community composition may be lost through generalization. Conversely, species-level discrimination was not necessary to illustrate differences between assemblages, so moderate levels of taxonomic resolution may be satisfactory. Species-level resolution might contribute substantially to habitat discrimination, but this remains to be tested.

The primary factor explaining differences between sites was the composition of the gorgonian assemblage; that is, the relative richness and abundance of genera on each site. This is illustrated by the overall richness and number of colonies/photo by site (Fig. 3) and by genus (Fig. 5), though interpretation of the MDS plots, and the pair-wise

comparisons. The BIO-ENV algorithm explained 92% of the variance between sites in terms of the three most abundant genera (*Ellisella*, *Nicella*, *Hypnogorgia*) and two less abundant genera (*Muricea*, *Caliacis*). Other genera (*Scleracis*, *Swiftia*, *Bebryce*) also attributed to a portion of difference in the iterations, so a good understanding of octocoral diversity contributes to better discrimination of the assemblages between features. Large sample sizes were also critical to the significance of the analyses.

One of the most useful and illustrative discriminations employed in this analysis was the comparison between sites using random, balanced groups of samples from similar depth ranges. The 50 - 60 m depth range was chosen to correspond with maximum depth of Stetson Bank, on the continental shelf. The range allowed comparison with photos of the Stetson Bank octocoral assemblage. No octocorals were found shallower than 52 m. The threshold corresponded with the maximum seasonal depth of the warm surface layer (50 -70 m), also known as the mixing layer (Rezak et al. 1985), so genera restricted to this range (*Muricea*, *Diodogorgia*, *Swiftia*) are subject to, and presumably adapted to high variability. The Stetson Bank assemblage was different for this reason, but the feature had a different geological origin, and the surrounding substrates were low relief, subject to sedimentation. The bank itself and the areal coverage of surveys were relatively small, so these factors together likely may explain the differences between Stetson Bank and other banks.

In contrast, the five other banks we studied were situated within 100 km of each other on the outer continental shelf break. WFGB, EFGB, Bright, Geyer, and McGrail had similar geological origin, similar size, similar peak heights, the same distance to the shore and the shelf break, with similar exposure to oceanic waters. By restricting our

comparison to the 50 – 60 m range, depth related factors were normalized. Still, the compositions of the assemblages at each site varied substantially. McGrail and Bright had no octocorals. WFGB was fairly rich (6 genera), while EFGB and Geyer were less so (3, 2 genera). Only one genus was shared between any two sites. Therefore, we speculate that site-scale variations in substrate, relief, exposure, and recruitment history (e.g. founder effects) were a better explanation for the observed distribution as opposed to large-scale phenomena, because corals were distributed broadly, but adjacent features were different. Research effort might confound our speculation, because the research design did not accommodate some important factors known to structure octocoral communities. Differences between banks may be explained by differences in substrate and exposure to high frequency and low frequency flows, like tides and upwellings.

Another surprising result of this study was the high average richness and abundance of octocorals between sites, relative to average richness and abundance on the banks themselves. There is a tendency to focus deep-coral research on prominent features with high relief, but low relief sites (2 - 40 m) between banks ranked among the highest for abundance and diversity. The composition of the assemblages was not significantly different than Bright or WFGB (Fig. 4), but richness and abundance were higher than expected. There was precedent for shared species between seamount features and the sites nearby (McClain et al. 2009), but there was no good precedent in the Gulf of Mexico for high octocoral richness on low relief features (2 - 40 m) besides the Mississippi Pinnacles (Gittings et al. 1992, see Fig. 1). The combination of results supports a broadly distributed octocoral habitat type on low relief features.

However, richness and abundance for sites between banks (EFB and WFGB) must be also considered in the context of habitat heterogeneity. Transects between EFGB and WFGB surveyed an extensive area of fine-scale patch reefs (2 - 10 m relief) and senescent mud volcanoes (20 - 40 m relief) that provided hard substrate and habitat for octocorals, black corals, sponges, and deeper water fish assemblages. The finding was contrary to the notion that sites between banks should be sub-optimal habitat because the substrates lacked substantial relief. The hard bottom patches were presumed to be drowned Pleistocene coral reefs that developed under conditions of lower sea stand (Rezak et al. 1985). Drowned reefs represent a majority of the deep-water habitat within FGBNMS perimeters, characterized in maps as “reefs... bearing a low diversity epifaunal community, including deep-water octocorals” (Rezak et al. 1985, p. 138).

Two mud volcano features captured in the between sites category were quite different. Mud Volcano One had only *Scleraxis*. Mud Volcano Two had moderate generic diversity (n = 6; *Chironephytha*, *Ellisella*, *Scleraxis*, *Muriceides*, *Nicella*, *Swiftia*). Other, more consolidated mounds of moderate relief were present within WFGB and EFGB. Southern Mound (50 m relief) was the hotspot for richness and abundance south of WFGB. Other small mounds (10 - 20 m) also had higher than mean abundance. This lends importance to the presence of low relief topography in deep water, because the expected benthic assemblage would be relatively diverse and abundant.

WFGB and EFGB both ranked highly in terms of richness and abundance. Within these sites we found clustered patterns with less than 1% likelihood that the pattern occurred as a result of random chance (Moran's I,  $p < .01$ ). These clusters occurred on mound features with moderate relief at the base of the banks, so hydrodynamic factors

associated with currents, sediment resuspension, and/or turbulence around deep topography (Genin 2003) might positively influence the abundance and richness of soft corals. Octocoral colonies are suspension feeders, so high particle flux should correlate with high growth and reproduction (Peccini & MacDonald, 2008), not necessarily high generic richness. However, swift currents will suspend sediments off hard substrate to expose substrates, and the increased habitat availability would be expected to increase the settlement potential for all genera, indirectly enhancing richness.

The prevailing currents on WFGB and EFGB are westward along the shelf break, but strongest currents are tidal fluxes from the north (Rezak et al. 1985, Cochrane & Kelly 1986). Hotspots (Figs. 6 & 7) were positioned near inflection points for impinging currents from the east and north. The bi-polar position of the hotspots was intriguing, because the pattern is similar to a butterfly pattern called ‘modified transient stability’ predicted in circulation models of weak flow over seamount features (Smith 1992, Goldner & Chapman 1997). Orographic effects induced by flows over and around a topographic feature might also result in leeward retention zones (Kelly et al. 2001), so further investigation of fine scale current flows and stratification around the banks may be warranted. The myriad effects of current flows on seamounts have been emphasized in recent research (Genin 2003). Studies are warranted because they would have application to dozens of similar features that occur along the shelf break (Fig. 1).

The photographic database technique highlights the value of large datasets, but also provides insight to research design. Our study began with 8495 images from seven different sites, but once duplicates, replicates, and images shallower than 50 m were removed, 5408 images remained, distributed unevenly between features. This large

number would appear to be sufficient until sites are compared, at which point the choice must be made to either drop the site with the lowest sample size (e.g., Geyer Bank) or to reduce the sample size to the largest common denominator (e.g. Geyer Bank, 91 images  $\geq$  50 m). For the ANOSIM statistics in the MDS plots, the effective comparison was between 90 images and 125 images from each site. Theoretically, the same results could have been accomplished with 650 – 2500 random images deeper than 50 m. Yet, this would require foreknowledge of a fine-scale depth threshold that could not be easily discerned without the original dataset of 8495 images. The overall data will be useful as they are applied to studies of other taxa.

As it stands, the database likely represents the largest compilation for mesophotic Gorgonacea in the world. The taxonomic resolution is noteworthy, though several morphotypes have yet to be identified. Most of the genera are known only from their original taxonomic descriptions, or from species lists in the Caribbean Sea (Cairns 2007b) and the Gulf of Mexico (Rezak et al.1985, Rezak et al.1990, Gittings et al. 1992, Reed et al. 2005, 2006), so the results are fairly novel for comparisons of the features, the assemblages, and the taxa represented.

Preliminary evidence that the community composition of mesophotic octocoral assemblages varies by bank and by depth was provided through these studies. Differences in abundance of a few common genera explained most of the variance, but at least one rare, indigenous genus (*Muricea*) was an important discriminator between study sites. Temperature variability associated with the relatively shallow depth of Stetson Bank explained the presence of *Muricea*, and the absence of cold-water genera less adapted to seasonally high temperatures. The scale of differences between balanced subsets of

seafloor images was 30 km. This was the distance between Bright Bank and EFGB, two features with the most similar profiles, and the most consistent differences.

At the outset of this manuscript, we introduced a null hypothesis of octocoral distribution seeking to clarify Bayer's (1961) remarks about the cosmopolitan distribution of deep-water gorgonians, and homogeneity of deep-water octocoral assemblages in the Gulf of Mexico. The underlying reason for our comparison was that a fundamental challenge for deep-water conservation and management under Bayer's hypothesis would be to confront the idea of a cosmopolitan deep-coral assemblage. Conservation initiatives typically prioritize measures of diversity, rarity, and endemism as the most efficient solutions to biodiversity protection (Myers et al. 1988, Roberts et al. 2002).

Here, the evidence supports variation in deep-coral diversity and abundance on spatial scales as fine as 30 km between sites, or 5 km within sites. Low-relief features (5 - 40 m relief) harbor a rich assemblage of octocorals, and larger features (WFGB and EFGB, 80 - 100 m relief) exhibit hotspots of deep-octocoral richness and abundance. If these results hold for other features, like seamounts, spatially explicit hotspots for octocorals can be expected, i.e. aggregations with above average richness and abundance. The distribution of octocorals may be cosmopolitan, but the composition of the assemblages does not appear to be homogenous. Therefore, place-based conservation of deep octocoral habitat is justified. Octocoral colonies create habitat for numerous associated species, so other taxa may be expected to co-vary with the octocoral assemblage. Future research should seek to establish patterns of connectivity and isolation between octocoral assemblages to better understand their ecology.

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## SUMMARY

This dissertation provided a brief review of the forces structuring shallow water octocoral communities, including depth, substrate, particle flux, exposure to currents, and periodic disturbance. The structuring forces were contrasted with a postulate introduced as Bayer's hypothesis, that below the warm water layer, deep octocorals are broadly distributed and cosmopolitan, with a homogenous distribution. This was a formalization of intermittent remarks by Dr. F. M. Bayer, Research Zoologist Emeritus, at the Smithsonian Institution National Museum of Natural History, intended to provide a theoretical framework to test distributional patterns of deep-adapted octocorals. The formalization and test of Bayer's hypothesis was not meant to disparage his legacy; Bayer himself recognized depth zones and provinces for octocorals, and he contributed immensely to our knowledge of West Atlantic octocorals.

Prevalence data for octocoral species (Chapter 1) and genera (Chapters 2 and 3) were employed with two independent variables, depth and location, to test:

- 1) differences in the assemblage composition between depth zones (Chapter 1);
- 2) differences between similar depths in different regions (Chapters 1 and 3);
- 3) differences in depth distribution between genera (Chapter 2);
- 4) differences in diversity and abundance between banks (Chapters 2 and 3).

Univariate tests, multivariate tests, and sample-based accumulation curves were applied to large, original datasets constructed for the purpose of this dissertation. The null hypotheses of no difference between banks, depth zones, and regions were rejected with confidence, because different techniques yielded the same result: different sites, depths, and regions had different octocoral assemblages. The results with octocorals were

consistent with patterns reported for other deep-water biota, specifically patchy distributions, and mid-slope peaks in diversity (Grassle & Morse-Porteous 1987, Rex 1981, Pineda & Caswell 1998).

Chapter One was a basin scale study with a second original database of 1881 unique octocoral occurrences derived from museums and cruise reports. Chapter Two used an original database of 8495 unique seafloor images to examine differences in octocoral diversity within and between banks in the northwestern Gulf of Mexico. Chapter Three analyzed the same photo database to discern the nature of the differences in diversity between banks. Over the course of this investigation, other tasks were accomplished that may have been lost in the deluge of information. I will attempt to highlight these in an effort to give support to lesser findings that may bear upon new understanding of the distribution and diversity of octocorals in the Gulf of Mexico.

Chapter One was an overview of the octocoral distribution and diversity in the Gulf of Mexico. The principal finding was a rejection of the null hypothesis of no difference between similar depth zones in different regions. This was a direct test of Bayer's postulate that, below the warm water layer, deep octocorals have a cosmopolitan distribution. Evidence of structure in the data was found to a depth of 1600 m, but there was no appreciable difference in diversity < 800 m, due to species replacement. Plots of the depth ranges for octocoral species and gorgonian genera illustrated shallow, intermediate, and deep taxa (Chap. 1, Figs. 4 & 7). At the deepest depths, structure was related to the relatively exceptional richness and abundance of octocorals in the Straits of Florida. Intermediate depths differed in terms of richness and abundance, as well as composition of the assemblages. Sea pens were prevalent near the Mississippi River.

The Mississippi River discharge may have affected octocoral richness and abundance, but it was difficult to distinguish river effects from research effort, because the basin scale data lacked null values. The basin scale database of 1881 records in Chapter One documented higher richness than 8495 seafloor photos in Chapters Two and Three, not surprising because of the difference in time span of the two databases (100 years vs. 5 years). Still, it was interesting that more records were available within Flower Garden Banks National Marine Sanctuary (FGBNMS) than the entire Gulf of Mexico. The northwestern upper continental slope, which encompasses FGBNMS was among the top 10 most diverse regions in the Gulf in terms of octocoral occurrences. This was not a function of unbalanced research effort within this study, because photo data from were not included in the basin scale meta-analysis. Research effort could have been relatively high on the northwestern upper continental slope, but this is suspect, because only one record occurred directly below the 50 – 200 m zone, in 200 – 800 m.

The primary finding in Chapter Two was that seven sites in the Northwestern Gulf of Mexico banks differed in terms of generic richness and diversity. A species list of octocorals from FGBNMS was constructed. The list was based on voucher specimens, available for molecular studies, and for comparison to other samples. A previous list was based on collections from other banks. Chapter Two called the term “Antipatharian Zone” into question, because highest richness was among octocorals. Octocorals and antipatharians co-occur in deep water so the more inclusive term “Deep Coral Zone” was recommended. The study lends empirical support to additional explorations. Bright Bank and McGrail Bank had high diversity. Bright Bank and sites between banks had higher

richness than expected given the effort invested. Generic richness and research effort were positively and highly significantly correlated.

Another relevant finding in Chapter Two was the recognition of a shallow group (comprised of *Diodogorgia*, *Muricea*, and *Swiftia*), and a deeper group (comprised of Ellisellidae, Nephtheidae, Paramuriceidae, and Primnoidae) with significantly different depth distributions. This was useful because octocoral depth ranges were typically provided as minima/maxima. The depth minima were consistent with the depth of the warm-water or mixing layer. High water temperatures were proposed to limit the upward distribution of deep-adapted species (Cary 1918, Bayer 1961) in an inversion of the classic depth and light limitations of zooxanthellate corals.

The principal results in Chapter Three were:

- 1) differences in octocoral richness and abundance between outer continental shelf (OCS) banks; and,
- 2) differences in the composition of octocoral assemblages between banks

Most of the variance between sites was explained by four abundant genera and one rare genus. Among the most abundant genera were *Ellisella*, *Nicella*, *Hypnogorgia*, and *Caliacis*. *Muricea* was a shallow genus found predominantly on Stetson Bank.

In Chapter Three, sites between banks were again shown to be nearly as rich and diverse and the banks themselves. The importance of this finding should not be underemphasized. There is a tendency to focus research on features with high relief, because research is expensive, and expectations of finding octocorals are high on prominences, due to accelerated currents and their related effects (Genin 2003). However, low relief features may be equally important to octocorals compared to high relief

features. Low relief features may provide ‘stepping stones’ for dispersal, as well as a surplus of habitat, because the areal coverage of low relief features would be expected to be greater than high relief features. Much of this habitat would be undetected, because high-resolution maps are necessary to resolve the low-relief habitat.

This dissertation elucidated some patterns of abundance, richness, and diversity for shallow and deep-water octocorals in the Gulf of Mexico, and in so doing, it drew extensively on the long history of research in the basin. Where progress was made, it was because of the concerted efforts of early explorers, natural history museums, taxonomists, students, professors, and federal employees. Shortcomings in the research partly reflected that so much more needs to be done in terms of mapping, taxonomy, species associations, ecological studies, and documentation. Novel methods and analytical techniques were tested, developed, and shared through this study with the hope that they will prove useful in applications elsewhere.

Octocorals were demonstrably widespread throughout the Gulf of Mexico, but their distribution was not homogenous. Assemblages varied by richness, abundance, and composition. Areas where richness and abundance were highest may represent optimal habitat for octocorals; it may be appropriate to seek protection from anthropogenic disturbance for these habitats, because numerous associated species would be expected to benefit. While octocoral habitat appears to be ubiquitous in deep water, optimal habitat appears to be rare, like old-growth forest amidst the woods.

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## APPENDICES

**Appendix 1. Scheffe's test for pair wise differences in diversity between depth zones.** The table shows depth zones (0 = 0 - 50 m, etc...), mean diversity per zone (Simpson's index, form  $1 - \lambda$ ), and the number of regional subunits averaged. Depth zones were highly significantly different (Kruskal-Wallis adjusted H,  $df = 4$ ,  $p < 0.01$ ). Bold matrix values show pairwise results above the critical value (Critical F = 2.536), therefore significantly different pairs at level  $p < 0.05$ .

**Scheffe's Test****Critical F = 2.536**

<b>Depth Zone</b>	<u>Diversity</u>	<u>N</u>	0	50	200	800
0	0.8844	13				
50	0.8936	13	0.0107			
200	0.7782	13	1.2874	1.5312		
800	0.7301	13	<b>2.7253</b>	<b>3.0748</b>	0.2662	
1600	<u>0.7252</u>	<u>9</u>	2.3747	<b>2.6695</b>	0.2647	0.0036

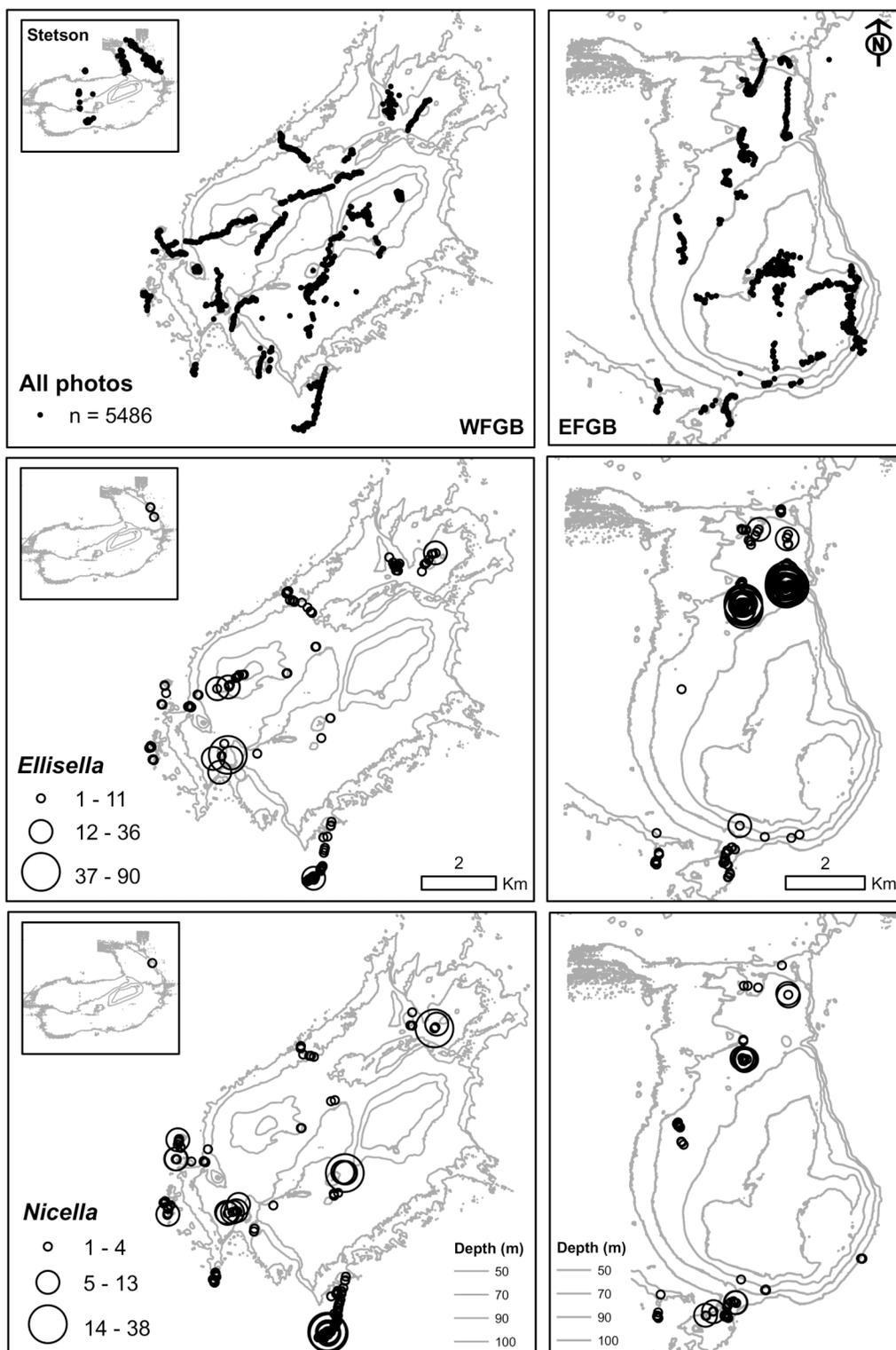
**Appendix 2. Scheffe's post-hoc test for differences between genera.** Scheffe's test uses a critical F value (F = 1.67, df between groups = 15, df within groups 1193, p < 0.05) to determine compare depth distributions between genera with unequal sample sizes. Values in bold indicate genera with depth ranges that differ significantly. Asterisk indicates genera with augmented sample sizes, the depth average includes some values interpolated from multibeam data (Gardner et al. 1998, Gardner & Beaudoin 2005).

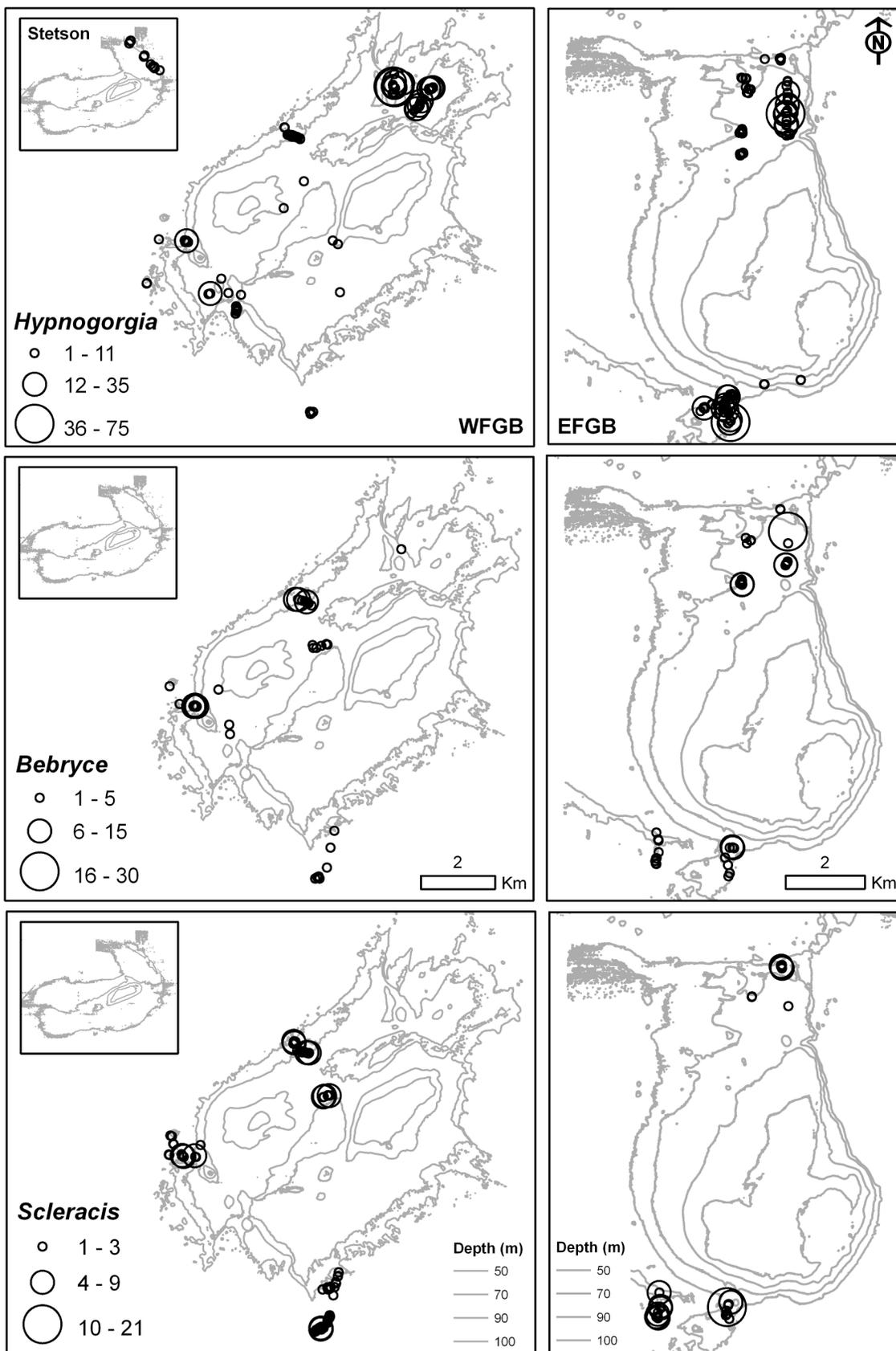
**Scheffe's Test**

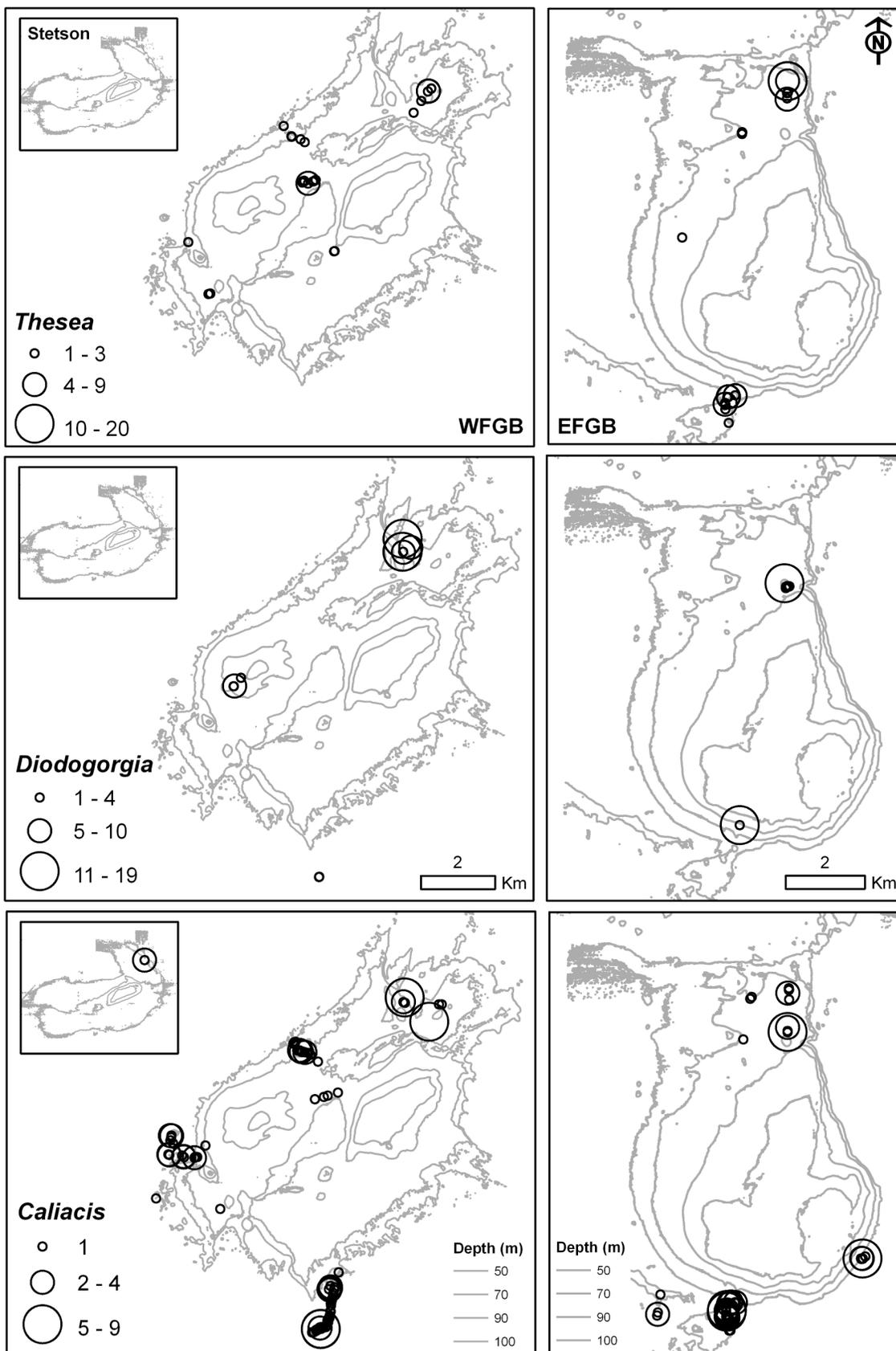
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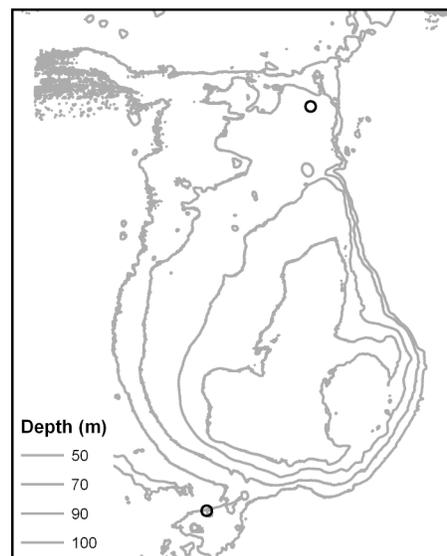
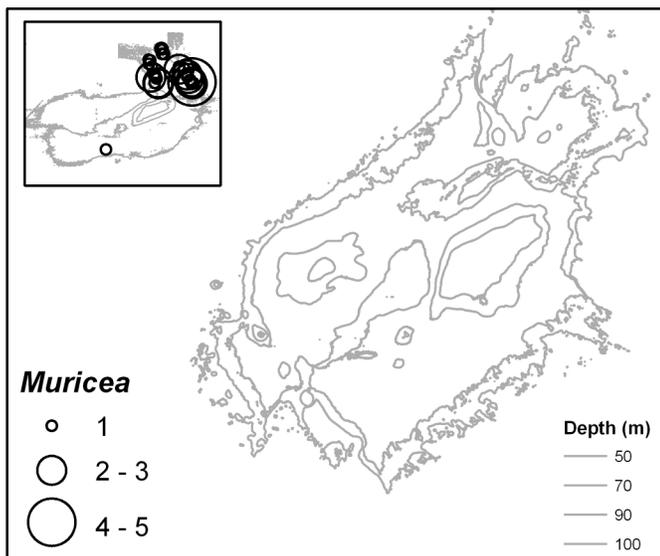
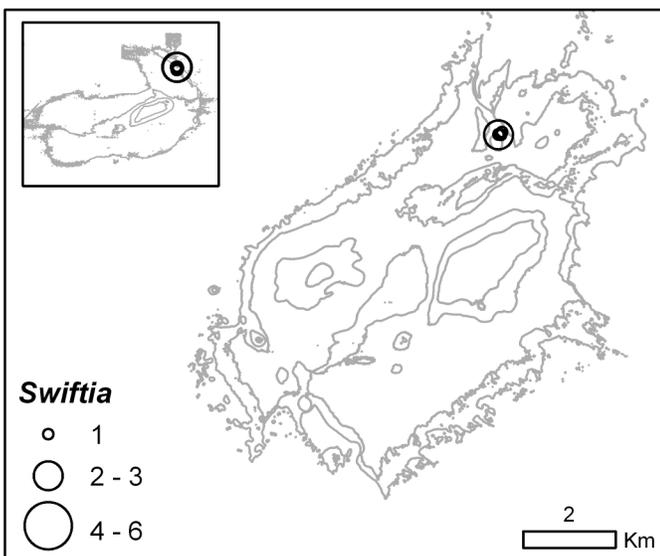
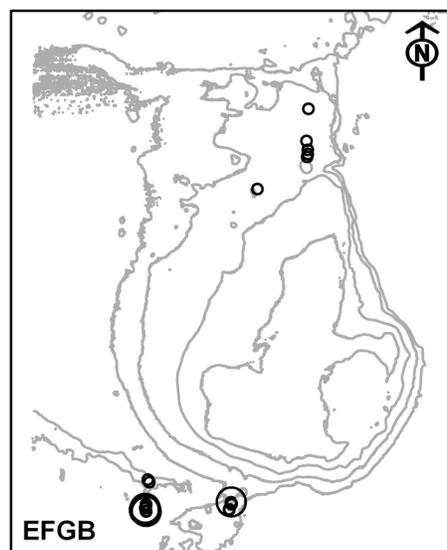
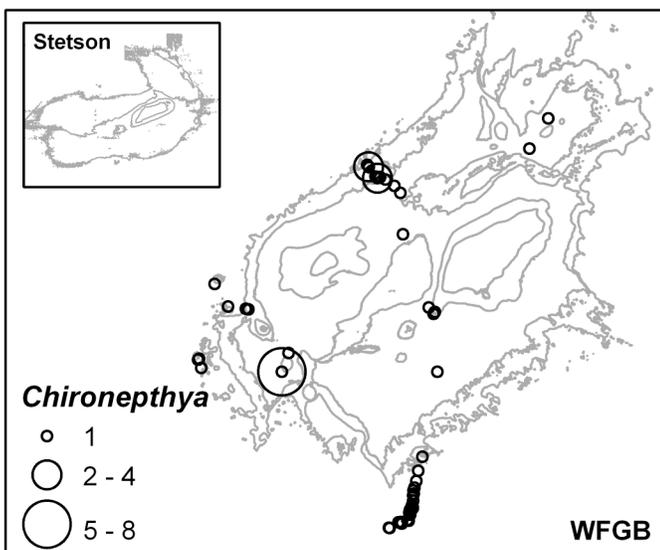
<b>Genus</b>	<b>N</b>	<b>Mean</b>	Bebry	Calia	Callo*	Chiro	Diodo	Elis	DF_16A*	Hypno	Muricea	Muriceid*	Nicella	Sclera	Swiftia	Thelo*	Thesea
Bebryce	73	89															
Caliacis	107	94	0.05														
Callogorgia*	41	102	0.66	0.23													
Chironophthya	52	97	0.24	0.04	0.09												
Diodogorgia	11	75	<b>2.24</b>	<b>3.81</b>	<b>8.92</b>	<b>5.95</b>											
Ellisella	250	80	0.16	0.27	1.46	<b>3.61</b>	0.25										
DF_16A*	43	98	0.33	0.07	0.07	0.01	<b>6.59</b>	0.97									
Hypnogorgia	183	82	0.08	0.19	1.17	<b>2.55</b>	0.62	0.01	0.74								
Muricea	28	56	<b>5.46</b>	<b>6.54</b>	<b>12.95</b>	<b>19.28</b>	<b>4.38</b>	<b>2.24</b>	<b>10.71</b>	<b>2.92</b>							
Muriceides*	61	104	0.75	0.31	0.03	0.56	<b>9.90</b>	1.30	0.16	1.09	<b>12.50</b>						
Nicella	142	97	0.15	0.02	0.07	0.00	<b>5.23</b>	0.36	0.00	0.28	<b>7.44</b>	0.12					
Scleracis	107	97	0.17	0.02	0.07	0.00	<b>5.36</b>	0.43	0.00	0.34	<b>7.85</b>	0.14	0.00				
Swiftia	26	71	<b>1.69</b>	<b>2.50</b>	<b>6.12</b>	<b>7.80</b>	0.15	0.31	<b>4.63</b>	0.57	<b>1.72</b>	<b>6.25</b>	<b>3.19</b>	<b>3.36</b>			
Thelogorgia*	10	98	0.97	0.21	0.19	0.00	<b>10.87</b>	<b>3.65</b>	0.00	<b>2.65</b>	<b>24.48</b>	0.49	0.01	0.01	10.29		
Thesea	48	86	0.03	0.17	1.14	1.41	1.58	0.11	0.65	0.04	<b>5.26</b>	1.27	0.35	0.38	1.39	<b>1.73</b>	
Unidentified	27	100	0.67	0.20	0.02	0.09	<b>8.71</b>	<b>1.80</b>	0.03	1.39	<b>14.54</b>	0.10	0.04	0.04	6.56	0.07	1.16

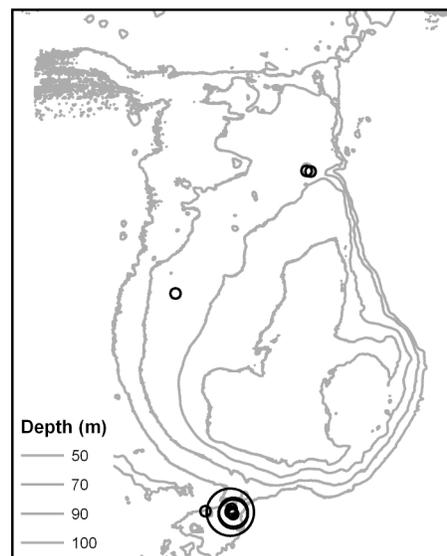
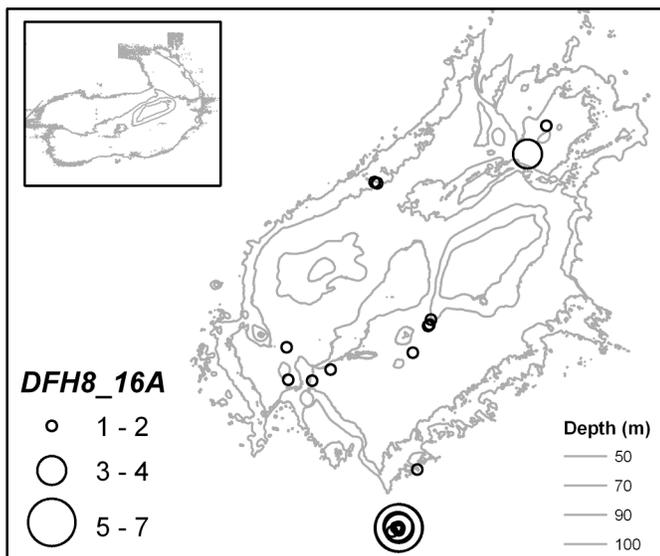
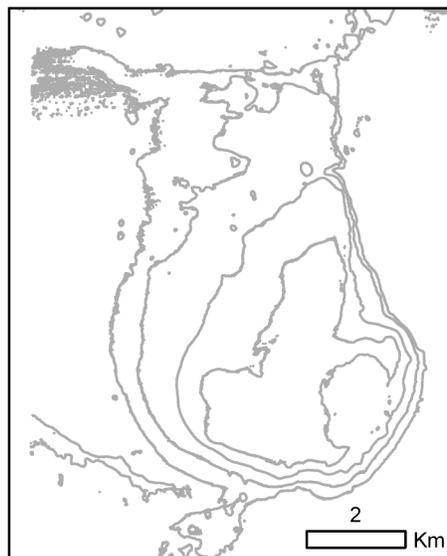
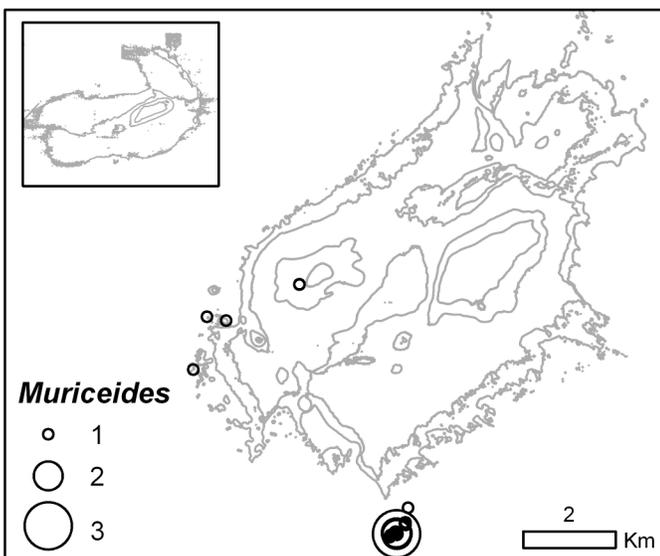
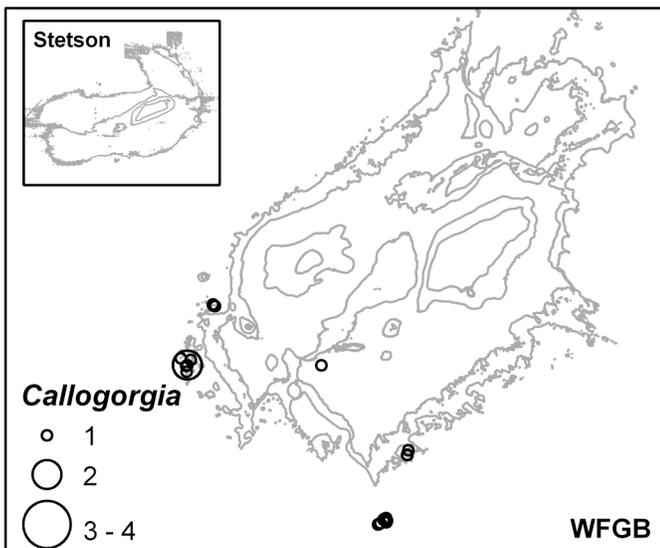
**Appendix 3. Maps of octocoral distribution on Flower Garden Banks.** The following maps show all photo locations (top panel, first page)  $\geq 50$  m in Flower Garden Banks National Marine Sanctuary (FGBNMS) - West Flower Garden Bank (WFGB), East Flower Garden Bank (EFGB), and Stetson Bank. Panels after the first show octocoral abundance by genus for each photograph. Null data for each genus may be inferred from the first panel in the first map.

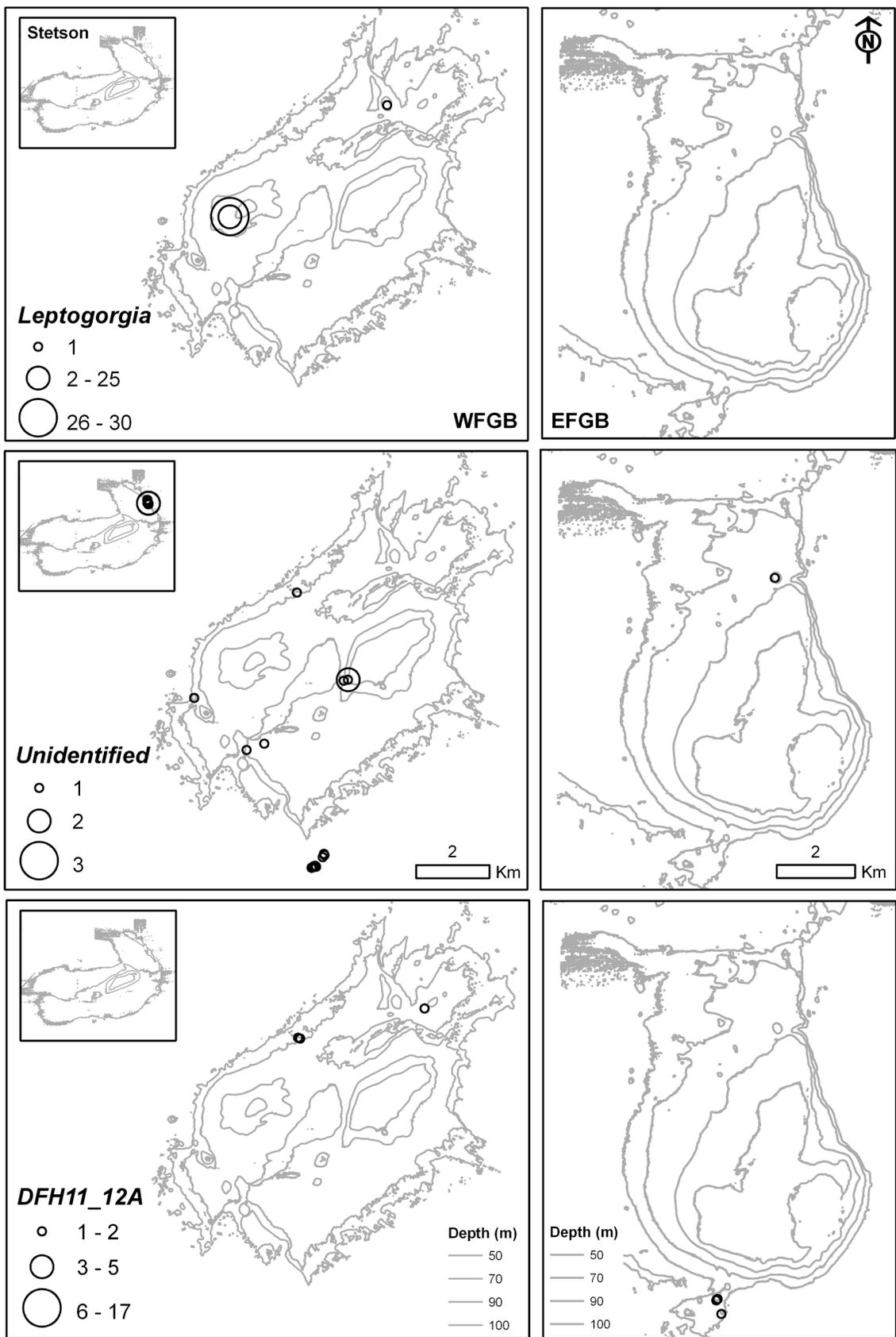


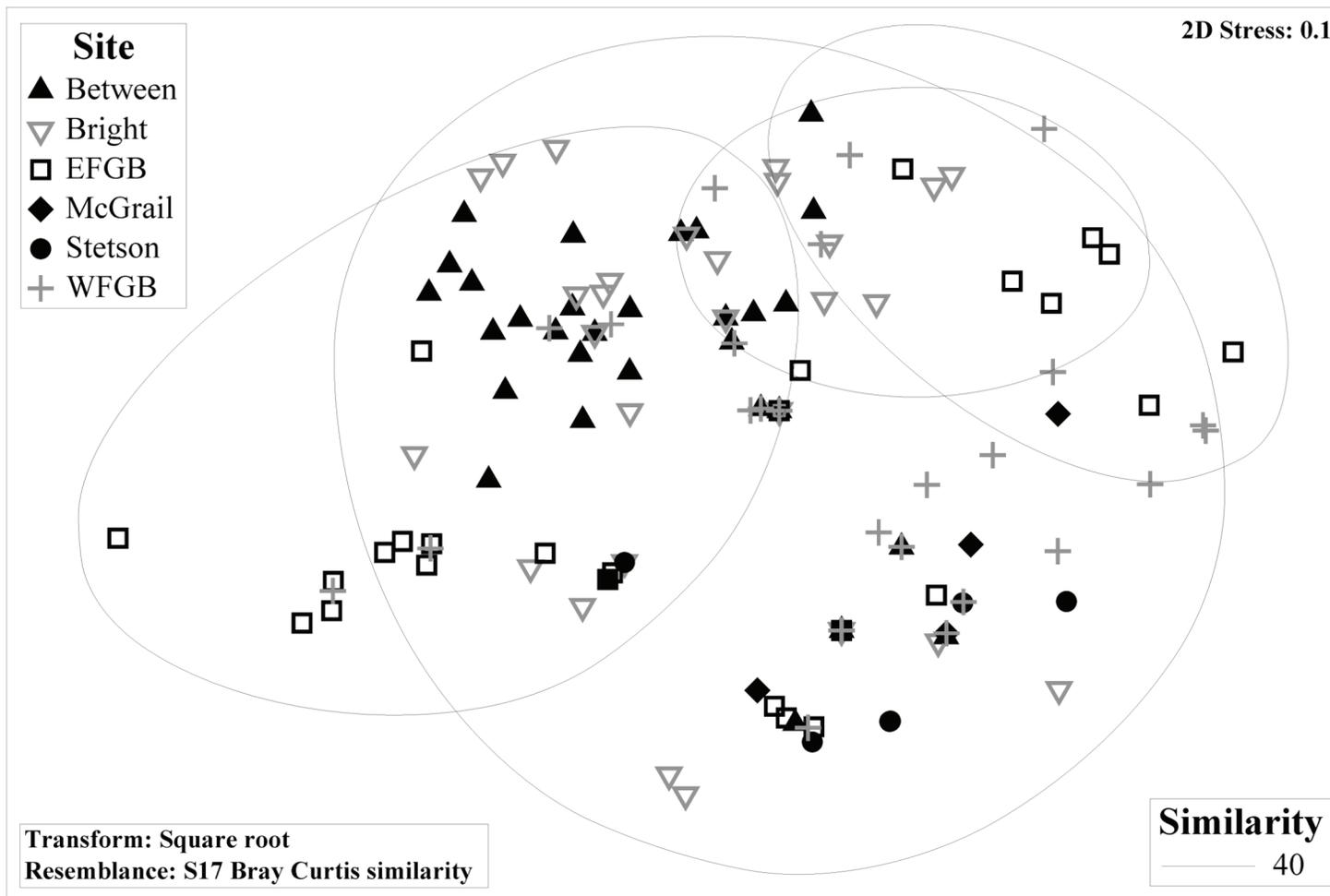












**Appendix 4. Ordination plot of all (n = 630) photo samples.** A non-metric multidimensional scaling (MDS) plot of Bray-Curtis similarity for zero-adjusted (+d), root-transformed abundance of 14 octocoral genera in a balanced set of 90 random photo samples from each study site (n = 7). The MDS plot is provided for comparison to the MDS plot for subsample means shown in Chapter 2, Figure 4. The 630 random samples are drawn from the larger photo-database of 5408 images  $\geq 50$  m. Many data points coincide, so they are overlaid on each other.

**Appendix 5. Scheffe's test for differences in mean richness and abundance per photo.** The results of pairwise tests (F values) for significant differences in mean richness and abundance of octocorals per photo at seven sites in the northwestern Gulf of Mexico. N = number of photo samples per site. **Bold** values indicate significant differences at level  $p < 0.05$ . WFGB = West Flower Garden Bank, EFGB = East Flower Garden Bank, Between = transects between banks.

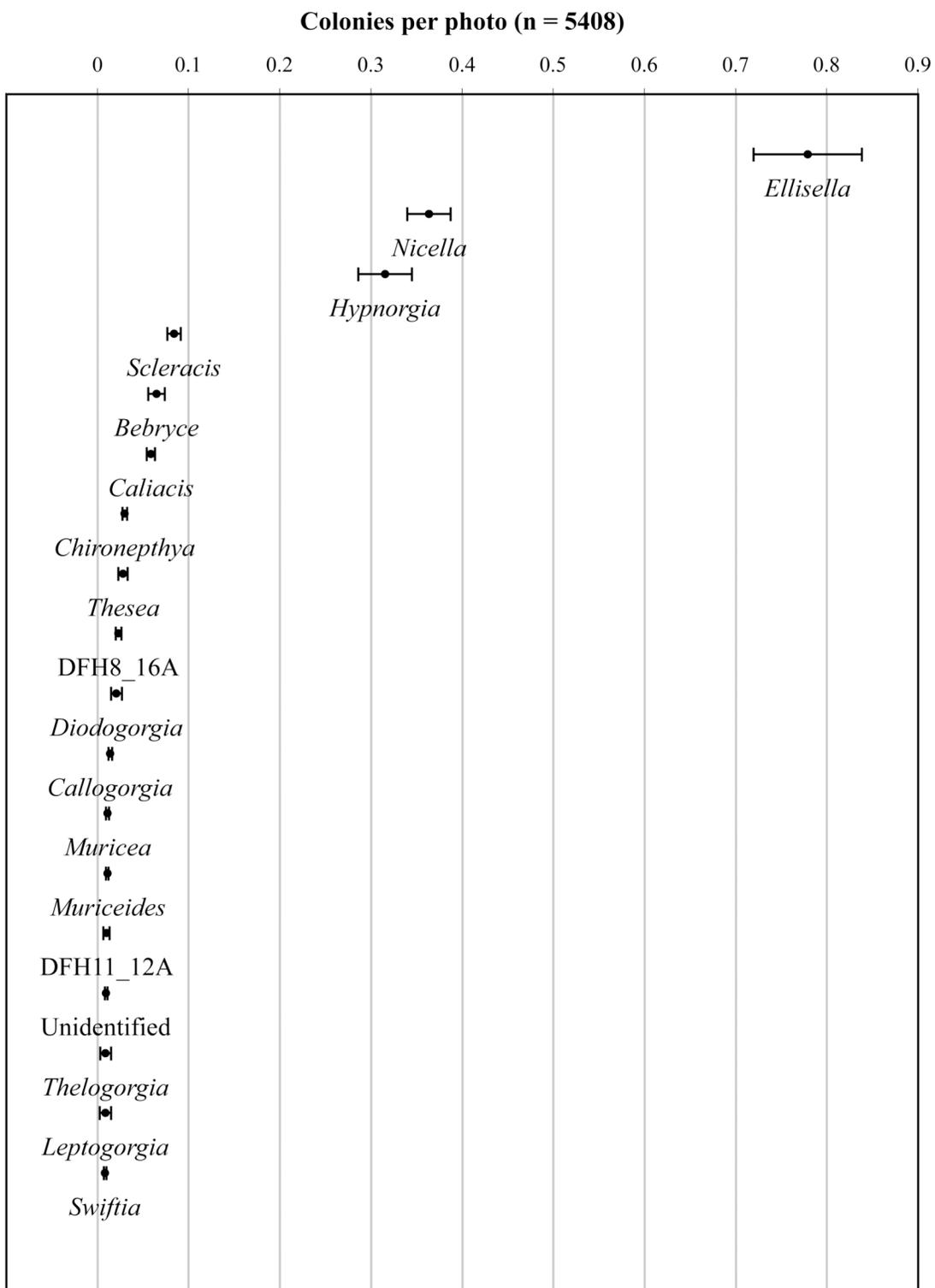
### Scheffe's Test

**Critical F = 2.099**

<b>Richness</b>	<i>Mean</i>	<i>N</i>	Stetson	WFGB	Between	EFGB	Bright	Geyer
Stetson	0.18	424						
WFGB	0.59	2031	<b>12.6</b>					
Between	0.81	322	<b>14.4</b>	<b>2.4</b>				
EFGB	0.45	1543	<b>5.4</b>	3.2	<b>7.3</b>			
Bright	0.66	216	<b>6.5</b>	0.2	0.6	1.6		
Geyer	0.42	91	0.8	0.5	<b>2.1</b>	0.0	0.7	
McGrail	0.24	781	0.2	<b>13.4</b>	<b>15.6</b>	<b>4.5</b>	<b>6.4</b>	0.6

<b>Abundance</b>	<i>Mean</i>	<i>N</i>	Stetson	WFGB	Between	EFGB	Bright	Geyer
Stetson	0.23	424						
WFGB	1.62	2031	<b>148.8</b>					
Between	3.23	322	<b>331.0</b>	<b>136.3</b>				
EFGB	3.04	1543	<b>570.2</b>	<b>355.4</b>	2.0			
Bright	1.64	216	<b>56.0</b>	0.01	<b>65.3</b>	<b>70.6</b>		
Geyer	2.80	91	<b>94.5</b>	<b>22.5</b>	<b>2.6</b>	1.0	<b>16.7</b>	
McGrail	0.25	781	0.02	<b>206.1</b>	<b>428.0</b>	<b>796.0</b>	<b>70.3</b>	<b>114.3</b>

**Appendix 6. Average abundance of octocorals by genus.** The chart pools abundance values from all images  $\geq 50$  m on all study sites ( $n = 5408$ ) to plot mean abundance and one standard error for 15 octocoral genera and two morphotypes (DFH\_16A, DFH11\_12A) commonly encountered on and around northwestern Gulf of Mexico banks. "Unidentified" groups several rare morphotypes.



## BIOGRAPHICAL STATEMENT

Peter J. Etnoyer was raised in Lancaster, Pennsylvania, with a background in math and sciences from Manheim Township High School. He switched to Liberal Arts early in his college career, graduating from Duke University in 1988 with a Bachelor of Arts in English and a Certificate in Film and Video Production. After a ten-year career working as a Camera Assistant and Art Department Coordinator on feature films in Hollywood, California, and commercials in Manhattan, New York, Peter returned to Duke University for a Master of Environmental Management. His thesis work examined the relationships between ocean circulation, coral reef area, and marine protected area coverage in the Caribbean and the Philippine Sulu Sea. Peter graduated from Duke University with an M.E.M. in 2001. During the period following he worked for the non-profit Marine Conservation Biology Institute mapping seamounts, deep-sea corals, ocean fronts, and marine mammals. The research led to his participation in research cruises with the submersible DSV *Alvin* and various remotely operated vehicles in the Gulf of Alaska and Gulf of Mexico. Peter started a family in Los Angeles, California, in 2005, and returned to school for a PhD at Texas A&M University- Corpus Christi. His research published in *Oceanography* and *Deep-Sea Research II* was awarded the NOAA David Johnson Award for Outstanding and Innovative use for Satellite Data in 2007.

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