**Benthic community composition of mesophotic coral ecosystems in the northwest Gulf of Mexico, with comparisons to Flower Garden Banks National Marine Sanctuary**

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Keywords: mesophotic coral ecosystems, northwest Gulf of Mexico, Flower Garden Banks National Marine Sanctuary, remotely operated vehicle, benthic communities, scleractinian

**Abstract**

Connectivity among mesophotic coral ecosystems (MCE), as well as connectivity between MCEs and shallow reefs, drive patterns of community structure, population persistence, and derived ecosystem services. Detailed benthic surveys combined with targeted molecular methods for characterizing mesophotic coral communities can contribute to the development of effective management strategies for these ecologically important, but threatened, coral reef ecosystems throughout the Tropical Western Atlantic.

**Introduction**

Assessments of geomorphology and benthic community structure have shown that mesophotic coral ecosystems (MCEs, 30-150 m) are distinct from their shallow water counterparts (Kahng et al. 2010, Lesser et al. 2009). For coral populations to become established in MCE locations, successful larval dispersal, recruitment, and maturation are required, with subsequent reproduction allowing these corals to contribute to the gene pool (Cowen et al. 2007). On the time scale of individual coral colonies (100s of years), these processes contribute to biodiversity in both coral community composition and intraspecific genetic diversity. At longer time scales, these processes control geographic distributions of species (Pulliam 1988) and the persistence of coral reefs in general. Elucidating these ecological patterns not only contributes to understanding of ecosystem processes and dynamics, but also provides critical information for the development of management strategies or predictive models. A comprehensive understanding of MCE connectivity requires assessment of: (1) the extent of MCE habitats and reef populations through time, (2) genetic connectivity among MCEs and shallow reefs, and (3) ability of MCEs to serve as larval sources for neighboring MCEs or shallow reefs.

The Gulf of Mexico has geological and oceanographic features that make it a unique system favorable to coral reef habitat and population persistence. Uplifted salt domes along the continental shelf margin in the NWGOM created numerous banks during the Jurassic period. These banks typically rise from the surrounding muddy seafloor to relatively shallow depths ranging between 17 – 50m, and many have carbonate caps (Hickerson et al., 2008; Precht et al., 2008). Similar reef habitats are also present along the drowned barrier reef structures of the West Florida Shelf in the southeast (SE) GOM (Jarrett et al., 2005; Reed, 2002). Habitats in the GOM are seemingly able to persist in part due to warm water delivered by three main currents: the Yucatan Current, Gulf of Mexico Loop Current, and Mexican Current (Ezer et al., 2005; Jarrett et al., 2005; Oey et al., 2005; Precht et al., 2014). The main path of these currents moves in a clockwise fashion from the Yucatan Peninsula, moving into the Straits of Florida (Lugo-Fernández, 1998). Additionally, eddy spinoff from the Loop Current occurs relatively frequently in the NWGOM and can persist for a year or more (Oey et al., 2005; Schmahl et al., 2008). As a result, the northwest NWGOM in particular remains a likely population source to downstream reefs due to its high coral cover and reproductive outputs, despite the low scleractinian species diversity (Hickerson et al., 2012; Jackson et al., 2014) and remoteness from its high latitude position (Rezak et al., 1990).

Models incorporating suitable depth zones and bottom substrates for MCEs estimated 178,867 km2 of potential mesophotic habitat in the Gulf of Mexico, two orders of magnitude greater area than the predicted 3,892 km2 habitat in the Caribbean or 3,299 km2 area in the Hawaiian Islands (Locker et al., 2010). This is logistically difficult to groundtruth, requiring resource-intensive exploration and characterization of the entire GOM continental shelf margin. MCE habitat availability is also likely reduced somewhat by turbid coastal waters (Locker et al., 2010), but is nonetheless predicted to have a high proportion of benthic habitat favoring scleractinian presence (Kinlan et al., 2013).

Approximately 150km off the coast of Galveston, Texas in the NWGOM, the FGBNMS includes West and East Banks (WFGB and EFGB, respectively). Residing on salt domes on the continental shelf, both banks are comprised of relatively shallow (17m) coral caps and surrounding mesophotic margin habitats to 50m (Clark et al., 2014; Hickerson et al., 2012). East of the FGBNMS, additional banks along the shelf margin provide habitat for mesophotic-only reefs at Bright (BRT) and McGrail (MCG) Banks, both of which are Coral Habitat Areas of Particular Concern (CHAPCs).

**Methods**

*Site selection and survey methods*

*Benthic community composition and statistical analyses*

Analyses of benthic communities in the NW GOM for 2014 and 2015 research expeditions followed the methods outlined in Voss *et al.* (2014) to allow comparability among 2010–2012 and 2014–2015 datasets. Transect photos were linked to georeferenced ROV dive tracks in an Access database. Data collection for percent cover and coral density were conducted in Coral Point Count with Excel Extensions v4.1 (CPCe; Kohler and Gill, 2006). Photos were first scaled using *in situ* scaled, parallel laser points in CPCe to generate image areas. Photos missing scaling laser points, or with significant reductions in image quality (*e.g.* incorrect altitude, blurriness, suspended sediment from ROV thrusters) were removed from subsequent analyses. Transects served as statistical replicates for both datasets. For percent cover, 50 points were randomly distributed over each photo and the benthic type under each point was identified. If no biota were present under a particular point, the benthos was characterized as soft or hard bottom. Biota were identified to the lowest taxonomic level possible, given the image quality. Scleractinian corals were identified to species, cnidarians in the Class Alcyonacea and Order Antipatharia were identified to family level, sponges were identified to Class, and algae to Phylum. All other categories were categorized into bacterial mat, Chordata, echinoderm, hydroid, Mollusca, and Tunicata groups. Dead coral was marked as different from hard bottom substrate, and a miscellaneous category was used for unidentifiable biota. Points that could not be identified at all, such as those in shadows or sediment plumes, were labeled as “tape wand shadow” and were removed from statistical analyses. The number of points corresponding to each benthic type were then summed across all photos per transect and divided by the total number of points to generate percent cover. For species density, all individuals of coral species (including scleractinians, soft corals, and black corals) were identified and counted per photo. Coral density was then calculated as the number of individuals m-2 for each species across the combined area of all photos in a transect. Both datasets were subjected to QAQC procedures to ensure correct identification of species, to verify consistency between 2010–2012 and 2014–2015 datasets, and to validate calculations of percent cover and coral density metrics. Both datasets were combined into a single dataset for statistical analyses.

All statistical analyses were conducted in the R statistical environment and Primer v7 and (Clarke et al., 2008; Clarke and Gorley, 2015; R Core Team, 2019). Due to violations of normality assumptions that could not be corrected with data transformation, nonparametric tests were used for both percent cover and coral density datasets. For percent cover, duplicate analyses were run on major taxa (Phylum level and general benthic type) and minor taxa (lowest taxonomic identification). Data were first standardized across transects, and square-root transformed to reduce influence of zero values found in many community datasets. Distance matrices were created for transects using Bray-Curtis dissimilarity for subsequent statistical and ordination analyses implementing non-metric multidimensional scaling (nMDS) with the R package *vegan* (Oksanen et al., 2019). Permutational analyses of variance (PERMANOVA; 9,999 permutations) were conducted using the *adonis* function in *vegan* to identify overall differences in benthic communities among banks. Following any significant PERMANOVA results the function *pairwiseAdonis* was used to conduct pairwise comparisons between banks, with false discovery rate (FDR) corrected *p*-values (Martinez Arbizu, 2017). Similarity percentage (SIMPER) tests were run in PRIMER v7 to determine the benthic taxa/types which contributed most strongly to community variation among sites using a similarity cutoff of 70%.

Additionally, richness, diversity, and evenness metrics were calculated for coral communities at all banks surveyed. Analyses were conducted for all corals (Orders Alcyonacea, Antipatharia, AnthoaXXX, and Scleractinia) at the Family level and for all Scleractinian corals to the genus level. Kruskal-Wallis tests were conducted for each metric to determine differences between banks. Following any significant tests pairwise Conover-Iman tests were implemented, using FDR corrected *p*-values.

**Results**

*Benthic percent cover*

Percent cover of benthic communities using major taxa was significantly different among sites (PERMANOVA: Pseudo-*F*4,295 = 21.118, *p* = 0.0001; Table ##), with significant pairwise differences primarily between sites outside FGBNMS (Bright, Geyer, and McGrail Banks) to those inside the sanctuary (West and East Flower Garden Banks). Pairwise comparison between West and East Flower Garden Banks was nonsignificant. PERMANOVA conducted on the minor taxa dataset corroborated the same trends for both main and pairwise tests (Pseudo-*F*4,295 = 35.508, *p* = 0.0001; Table ##). SIMPER results for major taxa indicated that benthic community variation among sites outside FGBNMS was largely driven by algal percent cover, while West and East Flower Garden Banks were differentiated by soft bottom cover (Table ##). Within minor taxa, algal groups *Chlorophyta* and crustose coralline algae (CCA) drove variation in benthic communities, with significant impacts from soft and hard bottom substrates at Bright and McGrail Banks, and soft bottom only at Geyer Bank. Benthic community variation at West and East Flower Garden Banks was once again attributed to soft bottom cover (Table ##).

Ordination of percent cover data within major taxa identified two main clusters at 60% similarity. One grouping was largely comprised of the majority of the West and East Flower Garden Banks transects, while the other group included transects from sites outside the sanctuary and the remaining FGB transects (Figure ##). Ordination of the minor taxa dataset suggested further differentiation within sites, with three main groups of transects clustering at 40% similarity. West and East Flower Garden Banks transects were splits into two of the three groups, while transects from outlying sites Bright, Geyer, and McGrail Banks separated into a distinct group (Figure ##).

*Coral species density*

Coral species density was significantly different across sites (PERMANOVA: Pseudo-*F*4,245 = 14.429, *p* = 0.0001), with all pairwise comparisons being significant, except between West and East Flower Garden Banks (Table ##). Variation in coral density among transects was driven by scleractinian (*Madracis* sp.), alcyonacean (*Leptogorgia* sp.), and antipatharians (Antipathidae, *Antipathes atlantica*, *A. furcata*, and *Stichopathes* sp.) for sites outside FGBNMS (Table ##). Variation in coral density in FGBNMS was driven mainly by alcyonacean (Ellisellidae and Plexauridae) and antipatharian (Aphanipathidae, *Antipathes* sp., and *Stichopathes* sp.). Ordination revealed weak grouping patterns among transects, with two main clusters at 20% similarity. Transects from outlying sites were found only in one of the groups, while transects from West and East Flower Garden Banks were found in the other group, with spread of some transects beyond the 20% similarity overlay (Figure ##).

**Tables and Figures**

Table 1. PERMANOVA results for percent cover and coral density datasets, with pairwise comparisons among sites. Nonsignificant p-values shown as ns.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Dataset** | **Level** | **Test** | **Comparison** | **Test statistic** | ***p*** |
| Percent cover | Major taxa | PERMANOVA | Site | 21.118 | 0.0001 |
|  |  | Pairwise | Bright Bank – Geyer Bank | 1.828 | 0.0393 |
|  |  |  | Bright Bank – McGrail Bank | 2.412 | 0.0079 |
|  |  |  | Bright Bank – East Bank | 5.367 | 0.0001 |
|  |  |  | Bright Bank – West Bank | 6.931 | 0.0001 |
|  |  |  | Geyer Bank – McGrail Bank | 1.498 | ns |
|  |  |  | Geyer Bank – East Bank | 4.871 | 0.0001 |
|  |  |  | Geyer Bank – West Bank | 6.566 | 0.0001 |
|  |  |  | McGrail Bank – East Bank | 3.963 | 0.0001 |
|  |  |  | McGrail Bank – West Bank | 5.404 | 0.0001 |
|  |  |  | East Bank – West Bank | 1.105 | ns |
|  | Minor taxa | PERMANOVA | Site | 35.508 | 0.0001 |
|  |  | Pairwise | Bright Bank – Geyer Bank | 2.215 | 0.0003 |
|  |  |  | Bright Bank – McGrail Bank | 2.034 | 0.0082 |
|  |  |  | Bright Bank – East Bank | 6.415 | 0.0001 |
|  |  |  | Bright Bank – West Bank | 7.590 | 0.0001 |
|  |  |  | Geyer Bank – McGrail Bank | 1.739 | 0.0374 |
|  |  |  | Geyer Bank – East Bank | 7.203 | 0.0001 |
|  |  |  | Geyer Bank – West Bank | 8.599 | 0.0001 |
|  |  |  | McGrail Bank – East Bank | 6.238 | 0.0001 |
|  |  |  | McGrail Bank – West Bank | 7.209 | 0.0001 |
|  |  |  | East Bank – West Bank | 1.208 | ns |
| Coral density | Minor taxa | PERMANOVA | Site | 14.429 | 0.0001 |
|  |  | Pairwise | Bright Bank – Geyer Bank | 2.125 | 0.0002 |
|  |  |  | Bright Bank – McGrail Bank | 1.495 | 0.0394 |
|  |  |  | Bright Bank – East Bank | 4.318 | 0.0001 |
|  |  |  | Bright Bank – West Bank | 3.991 | 0.0001 |
|  |  |  | Geyer Bank – McGrail Bank | 1.635 | 0.0193 |
|  |  |  | Geyer Bank – East Bank | 4.531 | 0.0001 |
|  |  |  | Geyer Bank – West Bank | 4.436 | 0.0001 |
|  |  |  | McGrail Bank – East Bank | 4.911 | 0.0001 |
|  |  |  | McGrail Bank – West Bank | 4.716 | 0.0001 |
|  |  |  | East Bank – West Bank | 1.306 | Ns |

Table 2. SIMPER results for percent cover and coral density datasets, with taxon/benthic type contributions shown in decreasing order within site. SIMPER cutoff was set to 70%.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Dataset** | **Level** | **Site** | **Taxon/Benthic type** | **Contribution** |
| Percent cover | Major taxa | Bright Bank | Algae | 63.61% |
|  |  |  | Soft bottom | 15.80% |
|  |  | Geyer Bank | Algae | 56.31% |
|  |  |  | Soft bottom | 22.73% |
|  |  | McGrail Bank | Algae | 42.76% |
|  |  |  | Soft bottom | 31.20% |
|  |  | West FGB | Soft bottom | 77.59% |
|  |  | East FGB | Soft bottom | 72.30% |
|  | Minor taxa | Bright Bank | CCA | 31.47% |
|  |  |  | *Chlorophyta* | 21.17% |
|  |  |  | Soft bottom | 14.22% |
|  |  |  | Hard bottom | 11.62% |
|  |  | Geyer Bank | *Chlorophyta* | 27.08% |
|  |  |  | CCA | 25.29% |
|  |  |  | Soft bottom | 18.73% |
|  |  | McGrail Bank | Soft bottom | 29.53% |
|  |  |  | CCA | 21.19% |
|  |  |  | *Chlorophyta* | 18.55% |
|  |  |  | Hard bottom | 13.03% |
|  |  | West FGB | Soft bottom | 78.60% |
|  |  | East FGB | Soft bottom | 73.42% |
| Coral density | Minor taxa | Bright Bank | *Madracis* sp. | 62.57% |
|  |  |  | *Leptogorgia* sp. | 8.90% |
|  |  | Geyer Bank | *Stichopathes* sp. | 30.22% |
|  |  |  | *Madracis* sp. | 18.69% |
|  |  |  | Antipathidae | 16.74% |
|  |  |  | *Leptogorgia* sp. | 11.21% |
|  |  | McGrail Bank | *Madracis* sp. | 40.77% |
|  |  |  | *Stichopathes* sp. | 19.09% |
|  |  |  | *Antipathes atlantica* | 7.94% |
|  |  |  | *Antipathes furcata* | 7.47% |
|  |  | West FGB | Ellisellidae | 29.02% |
|  |  |  | Aphanipathidae | 20.46% |
|  |  |  | *Stichopathes* sp. | 15.62% |
|  |  |  | *Antipathes* sp. | 12.10% |
|  |  | East FGB | Ellisellidae | 27.66% |
|  |  |  | *Stichopathes* sp. | 25.38% |
|  |  |  | Plexauridae | 20.25% |

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