# Fish community characterization of mid-shelf and shelf-edge mesophotic coral ecosystems in the expanded Flower Garden Banks National Marine Sanctuary

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coral reef paper

# Fish community characterization of mid-shelf and shelf-edge mesophotic coral ecosystems in the expanded Flower Garden Banks National Marine Sanctuary

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ABSTRACT.—The mid to outer continental shelf in the northern Gulf of Mexico is composed of a patchy distribution of coral and rock reefs designated high priority for marine protection. To better understand the influence of deepwater habitat on fish community dynamics and conservation needs, we compared altiphotic-mesophotic transition (20–40 m), upper mesophotic (40–60 m), and middle mesophotic (60–80 m) fish communities between mid-shelf (Sonnier Bank) and outer-shelf (McGrail Bank) banks from before their inclusion into the Flower Garden Banks National Marine Sanctuary. Surveys performed over two years with a remotely operated vehicle indicated that each bank and depth zone had distinct fish communities. Both banks were dominated by planktivores and piscivores, with an increase in depth specialists (e.g., deepwater anthiids and serranids) at the deeper zones surveyed, particularly in middle mesophotic depths at McGrail. An increased frequency of snappers, groupers, and amberjack was observed at Sonnier Bank, predominately in mesophotic depths, indicating the Sonnier Mesophotic Coral Ecosystem as either a hotspot or potential refuge for meso- and apex predators. This study fills a temporal gap in fish community dynamics of these two banks, serving to create a more continuous dataset available to assist in conservation assessments of the Flower Garden Banks National Marine Sanctuary.

Mesophotic coral ecosystems (MCEs) are deepwater habitats that have been proposed to function as distinct ecosystems due to shifts in environmental conditions with depth (light availability, temperature, seasonal variability, etc.) or deep refuges to vulnerable species from nearby shallow water reefs (Laverick et al. 2017, Baldwin et al. 2018, Rocha et al. 2018, Bongaerts and Smith 2019). Regardless of their specific ecosystem function, however, MCEs typically exhibit minimal tolerance to physicochemical fluctuations and slow growth and reproductive rates of associated organisms as a result of predominately cold, low productivity environments (Soares et al. 2020). Therefore, development of effective conservation policy for these ecosystems could benefit from further understanding of the ecosystem function each MCE provides.

The continental shelf in the northern Gulf of Mexico (GoM) is characterized by many biologically significant, patchily distributed reef covered structures, colloquially termed banks, that transition from altiphotic (<30 m) through mesophotic (40–150 m) depths (Rezak at al. 1985, NOAA 2016). These offshore banks provide critical habitat to many tropical species at the northern extent of their range, and therefore, develop fish communities that diverge from northern GoM nearshore waters (Dennis and Bright 1988). While the distance of these offshore banks from the coastline minimizes the magnitude of anthropogenic effects found on nearshore reefs, oil and gas (exploration and transport), fishing (commercial and recreational), and shipping activities (anchoring) still negatively impact their ecosystem structure and function (Hickerson et al. 2008, Lugo-Fernández and Gravois 2010, Etnoyer et al. 2016).

The Flower Garden Banks National Marine Sanctuary (FGBNMS) was established to protect the largest and most ecologically significant banks in the northern GoM and was recently expanded to include 14 banks in the region (NOAA 2016, Sammarco et al. 2016). Even with the recent expansion of the FGBNMS, there is limited understanding of fish community structures on high priority banks (Weaver et al. 2006). This is largely due to a discontinuous record of observations from 1986 to present. However, recent research suggests that banks at varying locations on the shelf may serve different ecological functions for reef fishes (settlement, growth, reproduction, etc.; Voss et al. 2014, Wetmore et al. 2020).

Here we attempt to fill in this discontinuous record by examining fish communities at Sonnier Bank and McGrail Bank (hereafter Sonnier and McGrail), two banks included in the recent expansion of the FGBNMS. The purpose of this study was to (1) describe and compare fish community structure between a mid-shelf bank (Sonnier) and outer-shelf bank (McGrail) and (2) contrast fish community structure between the altiphotic-mesophotic transition (20–40 m), upper mesophotic (40–60 m), and middle mesophotic (60–80 m) reefs with remotely operated vehicle (ROV) surveys.

## Methods

Study Sites.—Sonnier is a ring-shaped, mid-shelf bank that rises from a depth of 62 m to a crest at 20 m (Fig. 1). At Sonnier, ROV surveys centered on the six largest bathymetric features where two biologically distinct depth zones were evaluated: higher density *Millepora*–sponge habitat from 20 to 40 m and lower density habitat with antipitharians (*Cirripathes* sp.) from 40 to 60 m. McGrail is an outer-shelf bank with much deeper zones of significant reef-building corals found from depths of 60 m to the crest at 45 m (Fig. 1). At McGrail, surveys centered on the two shallowest peaks located on the southernmost ridge where two biologically distinct depth zones were evaluated: higher diversity habitat with reef-building corals from 40 to 60 m and deeper adjacent habitats dominated by rhodoliths from 60 to 80 m.

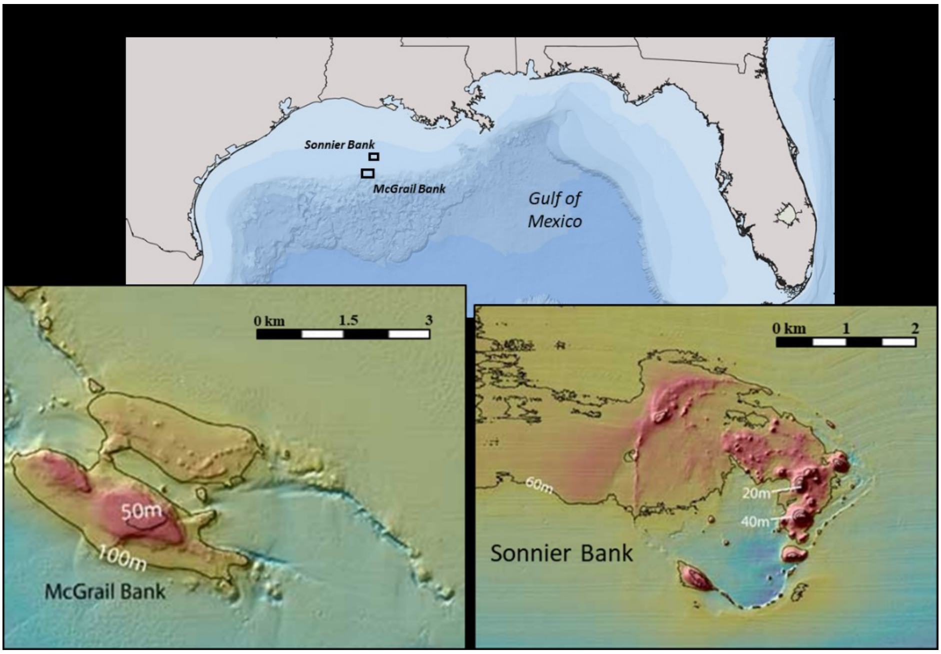


Figure 1. Locations and bathymetry of Sonnier Bank and McGrail Bank in the Gulf of Mexico. Surveys were conducted on pinnacle structures at Sonnier and the southern ridge at McGrail. Bathymetry images reproduced from Beaudoin et al. (2022).

Rov Surveys.—ROV roving surveys were conducted with an Inuktun™ Seamor ROV with a forward-facing camera. Surveys were started either at the base or crest of the reef, depending on depth stratification planned to sample, and followed a predetermined compass direction based upon the expected drift of the ship due to currents and local weather conditions. The live-boat method common in offshore surveys ensures the largest distance covered per ROV survey, but it does not allow for standardization of speed and depth as those are dependent on ship drift speed (Sward et al. 2019). The ROV was flown approximately 1–2 m above the bottom and deployments lasted 30–45 min. To standardize fish counts for comparison between deployments and sites, deployment videos were broken up into 3-min intervals, where each interval was treated as a roving transect. In each transect, total abundance was enumerated for each species identified, common for live-boat surveys in the FGBNMS (Weaver et al. 2006, Hickerson et al. 2008). To minimize the potential of double counting fish or large discrepancies in distance covered between transects, video footage while the ROV was stopped, descending, ascending, spinning, or when the camera was being zoomed was excluded from analysis. Surveys were conducted during two research cruises in August 2005 and June 2006, with each bank surveyed on both cruises.

Data Analysis.—Fish counts from ROV video footage were compared across banks and depth zones within banks using nonparametric multivariate ordination analysis in R, package vegan (Oksanen et al. 2017). Three depth strata (20–40 m, 40–60 m, 60–80 m) were selected a priori based on historical descriptions of shifts

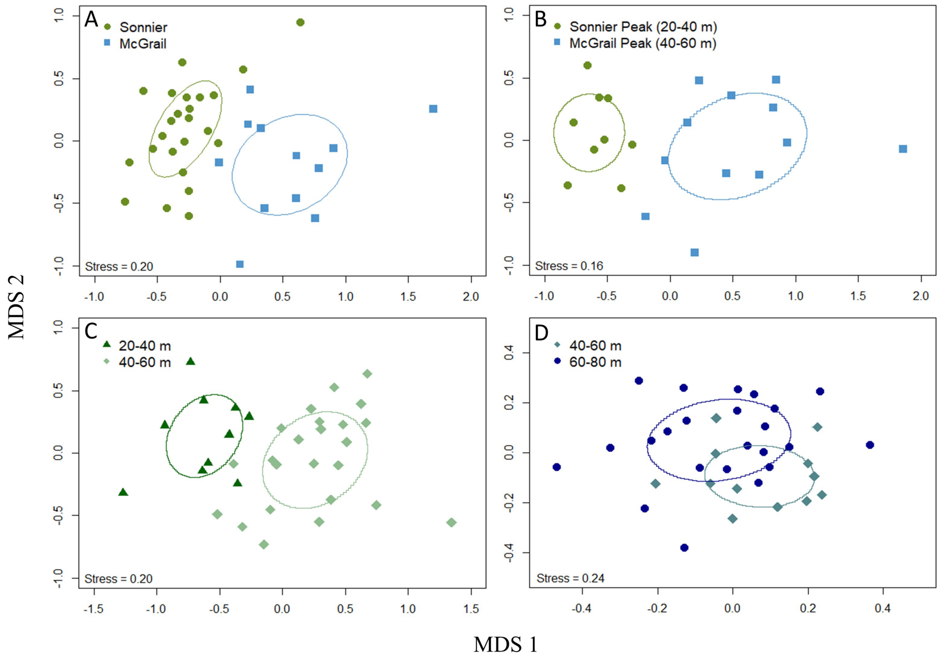


Figure 2. Nonmetric multidimensional scaling (NMDS) plots of fish community structure between (A) Sonnier Bank and McGrail Bank at 40–60 m depth, (B) Sonnier Bank and McGrail Bank structure peaks, (C) altiphotic-mesophotic transition (20–40 m) and upper (40–60 m) mesophotic depths at Sonnier Bank, and (D) upper (40–60 m) and middle (60–80 m) mesophotic depths at McGrail Bank. Stress values for NMDS ordination analysis given in the bottom left corner of each plot. Ellipses represent 1 standard deviation from the mean.

in habitat type and benthic composition at the two sites. Nonmetric multidimensional scaling (NMDS), multiresponse permutation procedures (MRPP), analysis of similarity (ANOSIM), indicator species analyses (ISA), and similarity percentages (SIMPER) were run on dissimilarity matrices calculated with Bray–Curtis distances to analyze differences in fish community structure ($\alpha$ = 0.05) between (1) Sonnier and McGrail at 40–60 m, (2) the Sonnier peak (20–40 m) and McGrail peak (40–60 m), (3) depth zones at Sonnier (20–40 m vs 40–60 m) and (4) depth zones at McGrail (40–60 m vs 60–80 m). For McGrail surveys at 60–80 m, the majority of fishes observed were unable to be identified to family or genus due to small size, ambient light, and distance from the ROV and therefore were removed from all analyses except mean abundance calculations.

## Results

At Sonnier a total of 34 transects were analyzed: 10 transects in the altiphotic-mesophotic transition zone and 24 transects in the upper mesophotic zone (Online Table S1). A total of 7033 fish from 60 species were observed: 2594 fish from 42 species in the altiphotic-mesophotic transition and 4439 fish from 42 species in the upper mesophotic. At McGrail a total of 35 transects were analyzed: 12 transects in the upper mesophotic and 23 transects in the middle mesophotic (Online Table S1). A

Table 1. Results for the indicator species analysis on (A) a comparison of upper mesophotic (40–60 m) fish communities between Sonnier Bank and McGrail Bank, (B) the altiphotic-mesophotic transition (20–40 m) and upper mesophotic (40–60 m) fish communities at Sonnier, and (C) the upper mesophotic (40–60 m) and middle mesophotic (60–80 m) fish communities at McGrail. IV = Indicator value statistic.

| A | Sonnier (40–60 m) | IV | *P*-value | McGrail (40–60 m) | IV | *P*-value |
|---|---|---|---|---|---|---|
| | Amberjack | 0.842 | <0.01 | Sargassum triggerfish | 0.866 | <0.01 |
| | Gray snapper | 0.764 | <0.01 | Sand tilefish | 0.645 | <0.01 |
| | Cocoa damselfish | 0.753 | <0.01 | Reef butterflyfish | 0.654 | <0.05 |
| | Blue angelfish | 0.736 | <0.01 | Barracuda | 0.500 | <0.05 |
| | Tomtate | 0.707 | <0.05 | | | |
| | Red snapper | 0.707 | <0.05 | | | |
| | Vermilion snapper | 0.612 | <0.05 | | | |

| B | Sonnier (20–40 m) | IV | *P*-value | Sonnier (40–60 m) | IV | *P*-value |
|---|---|---|---|---|---|---|
| | Brown chromis | 0.936 | <0.001 | Amberjack | 0.824 | <0.01 |
| | Bluehead wrasse | 0.896 | <0.001 | Yellowtail reeffish | 0.886 | <0.01 |
| | Spanish hogfish | 0.874 | <0.001 | Spotfin hogfish | 0.729 | <0.05 |
| | Bermuda chub | 0.837 | <0.001 | Red snapper | 0.707 | <0.05 |
| | Rock hind | 0.728 | <0.01 | Yellowmouth grouper | 0.677 | <0.05 |
| | Sergeant major | 0.632 | <0.01 | | | |
| | Blue runner | 0.632 | <0.01 | | | |
| | Bicolor damsel | 0.694 | <0.05 | | | |
| | Yellow jack | 0.548 | <0.05 | | | |
| | Dog snapper | 0.548 | <0.05 | | | |

| C | McGrail (40–60 m) | IV | *P*-value | McGrail (60–80 m) | IV | *P*-value |
|---|---|---|---|---|---|---|
| | Sargassum triggerfish | 0.727 | <0.05 | Threadnose bass | 0.780 | <0.01 |
| | Brown chromis | 0.577 | <0.05 | | | |
| | Purple reeffish | 0.500 | <0.05 | | | |

total of 13,452 fish from 46 species were observed: 1464 fish from 37 species in the upper mesophotic and 11968 fish from 30 species in the middle mesophotic.

Fish community structure was distinct between Sonnier and McGrail at upper mesophotic depths (MRPP: $P < 0.001$; ANOSIM: Global $R = 0.45$; Fig. 2A) and at structure peaks (MRPP: $P < 0.001$; ANOSIM: Global $R = 0.41$; Fig. 2B) with overall dissimilarities of 90.5% (SIMPER) between banks at upper mesophotic depths (Fig. 2A). The two most common fish at both banks were creolefish (*Paranthias fuscifer*) and yellowtail reeffish (*Chromis enchrysurus*). The Sonnier fish community was distinguished by three tropical reef-associated species [cocoa damselfish (*Stegastes variabilis*), blue angelfish (*Holacanthus bermudensis*), tomtate (*Haemulon aurolineatum*)] and four commonly exploited species [amberjack (*Seriola dumerili*), gray snapper (*Lutjanus griseus*), red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*)] (ISA: $P < 0.05$; Table 1A). The five most abundant fish were yellowtail reeffish, creolefish, tomtate, vermilion snapper, and gray snapper. In contrast, McGrail was distinguished by four ecologically unrelated species not commonly targeted by anglers [sargassum triggerfish (*Xanthichthys ringens*), sand tilefish (*Malacanthus plumieri*), reef butterflyfish (*Chaetodon sedentarius*), barracuda (*Sphyraena barracuda*)] (ISA: $P < 0.05$; Table 1A). The five most abundant fish were creolefish, yellowtail reeffish, brown chromis (*Chromis multilineata*), purple reeffish (*Chromis scotti*), and bicolor damselfish (*Stegastes partitus*).

At Sonnier distinct fish communities were identified at the different depth zones surveyed (MRPP: $P < 0.001$; ANOSIM: Global $R = 0.39$) with overall dissimilarities of 87.8% (SIMPER; Fig. 2C). At Sonnier, the altiphotic-mesophotic transition depth zone was distinguished by reef-associated tropical species [brown chromis, sergeant major (*Abudefduf saxatilis*), bicolor damselfish, bluehead wrasse (*Thalassoma bifasciatum*), Spanish hogfish (*Bodianus rufus*), Bermuda chub (*Kyphosus sectatrix*), blue runner (*Caranx crysos*), yellow jack (*Caranx bartholomaei*), rockhind (*Epinephelus adscensionis*), dog snapper (*Lutjanus jocu*)] (ISA: $P < 0.05$; Table 1B). The five most abundant fish were creolefish, blue runner, brown chromis, bluehead wrasse, and tomtate. The upper mesophotic zone was distinguished by three commonly exploited predators [amberjack, red snapper, yellowmouth grouper (*Mycteroperca venenosa*)] and two small depth specialists [spotfin hogfish (*Bodianus pulchellus*), yellowtail reeffish] (ISA: $P < 0.05$; Table 1B). The five most abundant fish were yellowtail reeffish, creolefish, tomtate, vermilion snapper, and gray snapper.

At McGrail distinct fish communities were identified between the two depth zones surveyed (MRPP: $P < 0.001$; ANOSIM: Global $R = 0.26$) with overall dissimilarities of 92.3% (SIMPER; Fig. 2D). The upper mesophotic was distinguished by two small pomacentrids [brown chromis, purple reeffish] and sargassum triggerfish (ISA: $P < 0.05$; Table 1C). The five most abundant fish were creolefish, yellowtail reeffish, brown chromis, purple reeffish, and bicolor damselfish. The middle mesophotic was distinguished by one small depth-specialist [threadnose bass (*Choranthias tenuis*)] (ISA: $P < 0.05$; Table 1C) that contributed 31% to overall dissimilarity. The five most abundant fish were threadnose bass, creolefish, yellowtail reeffish, bicolor damselfish, and yellowmouth grouper. However, due to our inability to identify a large number ($n = 8411$) of individuals in the middle mesophotic and the high stress value (0.24) in the ordination analysis, any conclusions should be considered provisional.

## Discussion

Differences in fish community structure between Sonnier Bank and McGrail Bank support a cross-shelf shift in fish communities between mid-shelf to outer-shelf banks in the Gulf of Mexico. Similar to previous descriptions, fish communities were dominated by tropical reef-associated species (Dennis and Bright 1988, Rooker et al. 1997, Wetmore et al. 2020), though with increased observations of mesopredators at Sonnier and depth-specialists at McGrail in this study. Increased abundances of these midsized predators at Sonnier may reflect species-specific habitat preference, a partiality for vertical structure, or result from differences in recruitment dynamics between mid- and outer-shelf banks (Kraus et al. 2006, Wetmore et al. 2020). Between 40 and 60 m depth, Sonnier is dominated by scattered antipatharian corals, gorgonians, and sponges commonly utilized by schooling omnivores and piscivores (Kraus et al. 2007, Sammarco et al. 2016). However, McGrail is composed of significant scleractinian coral coverage which locally accounts for up to 30% of benthic composition in the 40–60 m depth range and whose tri-dimensional complexity provides the necessary habitat for small reef fish (Rezak et al. 1985, Rooker et al. 1997, Weaver et al. 2006). In contrast to Sonnier, the most abundant fishes at McGrail were all small planktivorous anthiids and pomacentrids typically associated with hardbottom, vertical relief.

Shifts in fish community structure with increased depth are well-documented globally and at Sonnier and McGrail distinct fish communities were identified at the different depth zones surveyed, though specific depths of community break points were beyond the ability of our dataset to identify. At both sites the shift in fish communities occurred within a depth range (40–70 m) commonly documented in tropical and subtropical latitudes (Pinheiro et al. 2016, García-Hernández et al. 2018), including the GoM (Ajemian et al. 2015a,b). At McGrail the shift was indicative of the development of a unique fish community in the middle mesophotic dominated by depth specialists, similar to assemblage shifts at deep natural banks in the western GoM (Streich et al. 2017).

The upper mesophotic Sonnier fish community exhibited a clear increase in depth specialists but also included a significant increase in commonly exploited predators suggesting that the MCE may serve as a bright spot or refuge for species vulnerable to exploitation pressure. Considered a "nearshore" bank for the northern GoM, Sonnier is more commonly targeted by anglers and SCUBA divers (including spearfishers) than most banks in the FGBNMS. The MCE appears to be an important habitat for large predators, though it is unclear whether it functions as a release from fishing pressure at the structure peaks (temporary refuge) or a bright spot due to the healthy status of preferential habitat (area of residency; Bongaerts and Smith 2019). Consequently, the Sonnier MCE likely provides more than just a habitat for commonly exploited fishes but also top-down controls, an essential ecosystem function that is expected to become increasingly important as climate instability intensifies (Baum and Worm 2009, Papastamatiou et al. 2015, Lynam et al. 2017).

While limited in sampling scope, this study supports more recent mesophotic and cross-shelf fish community comparisons described for the Gulf of Mexico (Voss et al. 2014, Streich et al. 2017, Wetmore et al. 2020). The surveys indicate that a shift in composition occurs at both banks as depth increases, with the MCE at Sonnier potentially serving as a bright spot or deep reef refuge for commonly exploited fish species (Baldwin et al. 2018, Bongaerts and Smith 2019). If the mesophotic ecosystem at Sonnier does serve as a bright spot or refuge, through proper conservation it can improve ecosystem resilience in the face of stochastic perturbation (Laverick et al. 2017, Rocha et al. 2018) and a changing climate regime (Lynam et al. 2017) by preventing the cascading effects associated with predator release (Heithaus et al. 2008).

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