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Steven B. Garner [a,*], Kevin M. Boswell [b], Justin P. Lewis [a], Joseph H. Tarnecki [a], William F. Patterson III [a]

[a] University of Florida, Fisheries and Aquatic Sciences, 7922 NW 71st St, Gainesville, FL, 32653, USA
[b] Florida International University, Biscayne Bay Campus, 3000 NE 151st St, North Miami, FL, 33181, USA

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ABSTRACT

Reef fish resources provide numerous ecosystem services in the northern Gulf of Mexico (nGOM) large marine ecosystem. Artificial reefs (ARs) have been distributed across the nGOM in attempts to enhance reef fish habitat and increase fishery productivity, but few data exist to distinguish ecological from fishery functions of ARs compared to natural reefs (NRs), particularly at the regional scale. Therefore, we conducted remotely operated vehicle surveys of reef fish communities at 47 reef sites within a ~20,000 km^2 area of the nGOM shelf and tested the effect of reef type (NR versus AR), depth (≤35 or >35 m), relief (≤2 m or >2 m), and complexity (low or high) on fish diversity and community structure as well as trophic guild- and species-specific densities. Twenty-one species were present at >20%, nine at >50%, and three at >75% of study reefs. Fishery species (i.e., *Lutjanus campechanus*, *Seriola dumerili*, and *Rhomboplites aurorubens*) and invasive *Pterois volitans* were frequently observed (>50% of sites) or numerically dominant, especially at ARs. Main effects did not significantly affect the presence of specific species or trophic guilds, but interactions among factors significantly affected species- and trophic guild-specific densities. Our results indicate that effects of habitat characteristics on fish communities are more nuanced than previously described. Fish communities are moderately similar at the majority of sites but specific habitat characteristics can interact to dramatically affect densities of some species, particularly those that depend on complex structures for refuge. Simple ARs tend to concentrate high densities of a few important fishery species with low densities of other small demersal reef fishes. Complex NRs with high relief also support high densities of planktivorous fishery species but greatly increase densities of small, demersal, non-fishery species that directly utilize complex reef structure for refuge.

1. Introduction

Reef habitats are critical components of the northern Gulf of Mexico (nGOM) large marine ecosystem (LME) that provide both ecological (Worm et al., 2006; Granek et al., 2010; Barbier et al., 2011) and cultural (Holland and Ditton, 1992; Abson and Termansen, 2011) ecosystem services (Costanza et al., 1997; Farber et al., 2006). Reef structures provide food, shelter, and nursery habitat for ecologically important fishes and invertebrates (Dennis and Bright, 1988; Koenig et al., 2000), enhance nutrient cycling (O'Neil and Capone, 2008; Kellogg et al., 2013), and support the economies of coastal communities through fishing and tourism. Found across the continental shelf, natural reefs in the nGOM primarily consist of relic shorelines and biogenic limestone reefs from the Pleistocene epoch or late Quaternary period (Thompson et al., 1999; Gardner et al., 2005; Hine et al., 2008). Light penetration at upper and mid mesophotic reefs (40–80 m) combined with nutrient-rich freshwater inputs can support rich communities of both photosynthetic and azooxanthellae corals and invertebrates (Hinderstein et al., 2010; Locker et al., 2016) with diverse fish assemblages (Dennis and Bright, 1988; Allee et al., 2012; Patterson et al., 2014; Streich et al., 2017).

Reef fish resources are a major driver of nGOM coastal economies. Reef fish resources support nearly 200,000 fishing related jobs in Florida alone with the marine economy of all US Gulf states valued around $3 trillion (NMFS, 2016). However, the life history characteristics that facilitate reef fish evolutionary success and annual productivity also make reef fishes susceptible to a variety of anthropogenic and environmental stressors (Coleman et al., 1999; Coleman and Koenig, 2010), such as oil spills (Tarnecki and Patterson, 2015; Joye et al., 2016;

* Corresponding author. 7922 NW 71st St, Gainesville, FL, 32653, USA.
E-mail address: sgarner@ufl.edu (S.B. Garner).

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Murawski et al., 2016), harmful algal blooms (Smith, 1979; Coleman and Koenig, 2010; Dupont et al., 2010), biological invasions (Dahl and Patterson, 2014; Chagaris et al., 2017), and overfishing (Coleman et al., 2004; Cowan et al., 2011). Artificial reefs have been deployed throughout the GOM in an attempt to enhance reef fish productivity, but their potential benefit may be outweighed by increased catchability (Campbell et al., 2011; Cowan et al., 2011) and the low proportional contribution of ARs to reef fish production compared to more expansive NR habitats (Karnauskas et al., 2017).

Despite the ecological and economic importance of reef habitats, few comparisons exist to assess ecological differences between reef types (AR versus NR) and potential drivers of community or trophic structure in this system. Previous research on hard-bottom habitats has focused on characterizing reef fish communities at unique natural formations because of their high species diversity and importance as reef fish spawning sites (Rooker et al., 1997; Koenig et al., 2000). Recent studies of reef fish community structure in the nGOM have primarily focused on the potential for oil and gas platforms and other ARs to serve as fisheries enhancement tools (Lingo and Szedlmayer, 2006; Dance et al., 2011; Ajemian et al., 2015) and did not include direct comparisons with NRs. Currently, inferences regarding drivers of community structure, trophic structure, and potential ecological differences between habitat types must be derived from spatially and temporally disconnected studies scattered throughout the nGOM region.

The purpose of this study was to examine differences in reef fish community and trophic structure between NRs and ARs on a regional scale while accounting for the effects of different reef characteristics. Specifically, we sought to quantify the species-and trophic guild-specific density of fishes present at reef structures throughout the study area, and then test the effect of reef type, water depth, and reef morphology (i.e., relief and complexity) on those parameters. Study results help elucidate the factors driving differences in reef community and trophic structure at reefs across the nGOM to help fishery managers better design and deploy ARs to maximize ecological functionality rather than simply to increase fishing opportunities. These data also provide important baseline information to help fishery managers monitor changes in community structure in response to acute or chronic anthropogenic stressors.

2. Materials and methods

Sampling was conducted onboard chartered fishing vessels with home ports in Orange Beach, Alabama, Pensacola, Florida, or Destin, Florida. Study reefs were located on the central nGOM continental shelf offshore of Perdido Key to Cape San Blas, Florida (−88.5 to −85.5 °W longitude; Fig. 1). The study area is in a geological transition zone from west to east due to the decreasing influence of the Mississippi River and other freshwater outflows that deposit fine-particle sediments (Thompson et al., 1999). With eastward longitude, bottom sediments increase in grain size and transition from silica quartz to carbonate sands, primary productivity decreases, and bottom complexity increases due to prevalence of limestone outcroppings and reduced sedimentation rates (Thompson et al., 1999). Reef sites (AR or NR) were randomly selected from two depth zones [shallow (≤35 m) or deep (>35 m)], relief levels (low, ≤2 m or high, >2 m), or complexity levels (low or high) and were surveyed once each during May through October 2017. Simple structures comprised of concrete or metal with few holes or refugia were classified as low-complexity ARs (Fig. 2A, C); structures comprised of multiple units forming a debris field with many holes or interstitial spaces were classified as high-complexity ARs (Fig. 2B, D). High-complexity ARs also often had well-developed invertebrate fouling communities that added additional complexity. Natural reefs classified as low complexity also had few holes or ledges or consisted of relatively flat carbonate rock surfaces (Fig. 2E, G), while high-complexity NRs had complex rock outcroppings or ledges with many holes or crevices for refugia and often had dense fouling communities (Fig. 2F, H).

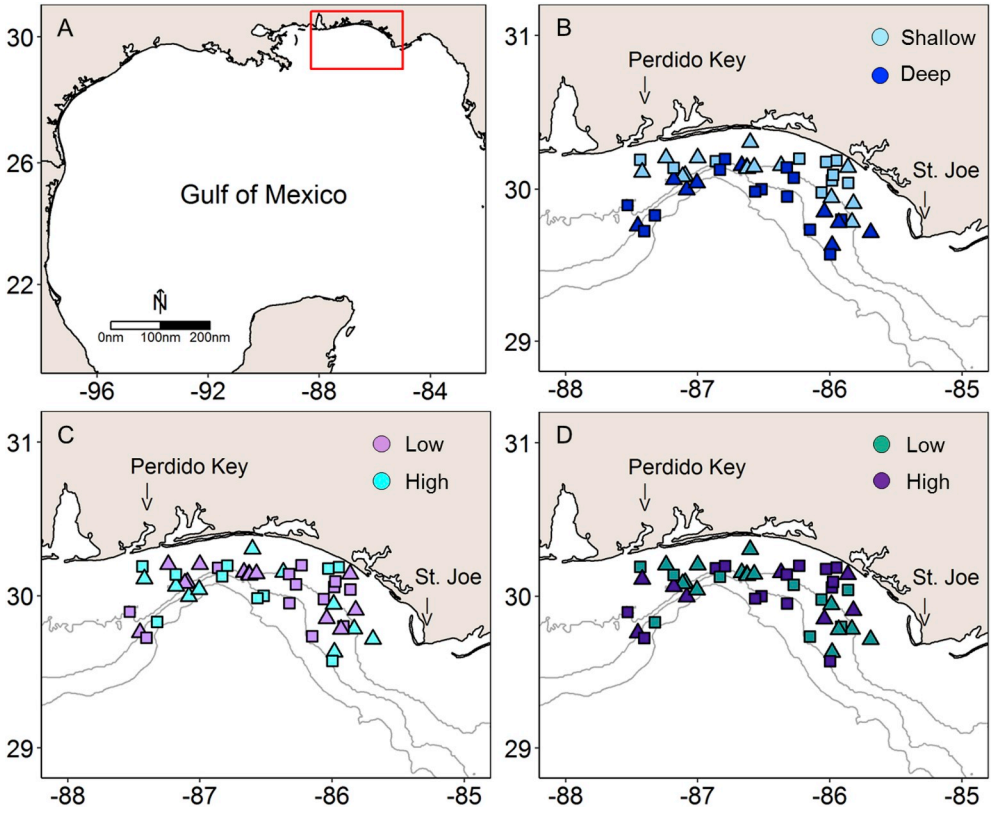

Fig. 1. Geographical location of reef sites sampled in 2017 in A) the northcentral Gulf of Mexico (red box). Artificial (triangles) and natural (squares) reefs were sampled at two B) depth zones (shallow, ≤35 m or deep, >35 m), C) relief levels (low, ≤2 m or high, >2 m), or D) complexity levels (low or high) located offshore between Perdido Key and Port St. Joe, Florida. The 35, 50, 100 m isobaths are indicated in panels B–D. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

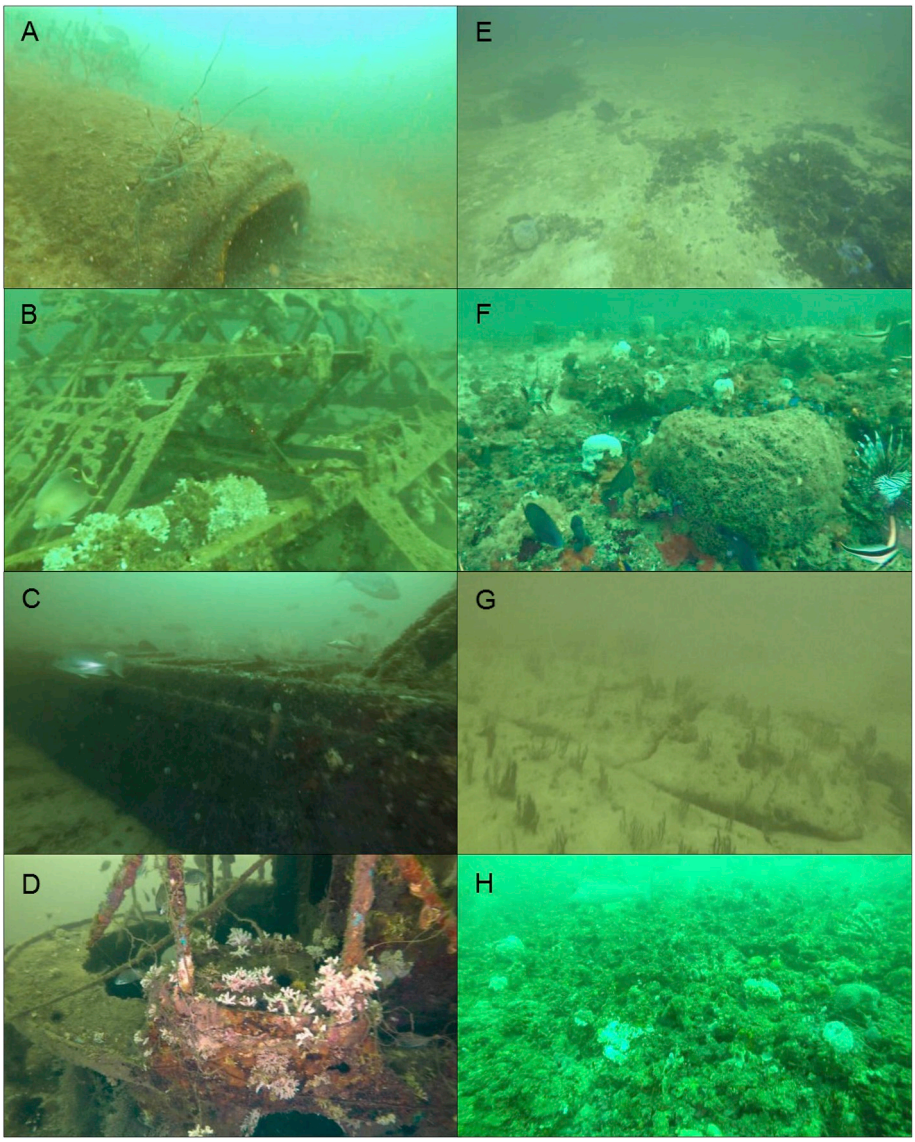

Fig. 2. Artificial (panels A–D) or natural (panels E–H) reef sites surveyed with ROVs in 2017 with low relief (≤2 m) and low complexity (A and E), low relief and high complexity (B and F), high relief (>2 m) and low complexity (C and G) or high relief and high complexity (D and H).

2.1. ROV sampling protocols

Fish communities were surveyed with a VideoRay Pro4 mini remotely operated vehicle (ROV). A modified point-count method, described by Patterson et al. (2009) and adapted from Bohnsack and Bannerot (1986), was used at ARs with relatively small benthic footprints (e.g., single or paired concrete pyramids or reef balls). Transect surveys, as described by Patterson et al. (2014), were used at all NRs and spatially expansive ARs (e.g., haphazardly spaced aggregations of artificial structures or debris fields). With the modified point-count method, species-specific counts were made in a 15-m wide cylinder by first performing 360° spins with the ROV parallel to and 1 m above the seafloor on opposite sides of the reef module, with the module positioned at the center of the surveyed area. Prior to each spin, the ROV was positioned approximately 5.5 m from the module's base, thus providing an estimate of the cylinder's radius when calculating the total area surveyed (Patterson et al., 2009). The ROV was then flown to 1 m above the module followed by 10 m above the module where additional 360° spins also were made. Species-specific counts were summed across all spins (counts for spins made 1 m above the seafloor were only made for fish located on the same side of the AR module as the ROV) and divided by the total area surveyed (176.7 m^2) to estimate species-specific density (fish•m^{-2}). With the transect method, species-specific counts were derived by flying four orthogonal 25-m long transects from a fixed point on the seafloor. A 3 kg clump weight attached to the ROV's tether designated the common origin point of all four transects. Transect diameter was estimated given ROV's height off bottom (1 m), the angle of the camera (45°) relative to the seabed, and the field of view (116°) of the camera (Patterson et al., 2014). Species-specific counts were summed across the four transects and divided by the total area surveyed to estimate species-specific density (fish•m^{-2}). Transect area was calculated by multiplying the transect width by length; total area surveyed was the sum of the four transect areas at a given reef.

An external camera (GoPro Hero 3 + or 4) attached to the ROV provided high-definition video (2.7k resolution at a frame rate of 60 fps) to maximize species identification and measurement accuracy during video sample processing. Digital video was analyzed in the laboratory to estimate reef fish community structure. All fishes observed during ROV surveys were identified to the lowest taxonomic group possible and enumerated.

2.2. Statistical analyses

Differences in community structure were tested between habitat types, depth zones, relief levels, and complexity levels with a four-factor permutational multivariate analysis of variance (four-way PERMANOVA; $\alpha = 0.05$) in Primer with PERMANOVA+ (Anderson et al., 2008), with species-specific densities (fish•10^3 m^{-2}) as the dependent variables. A Bray-Curtis dissimilarity matrix was calculated with 4th-root transformed densities among samples. Permutational tests of homogeneity of dispersions were performed on deviations from centroids for each of the four factors with the PERMDISP procedure. Dissimilarity percentages were estimated with the SIMPER procedure to compare species-specific contributions to dissimilarity for significant main effects or interactions in each model. Community structure also was compared by assigning species-specific ranks (1…N, where N is the total number of species observed across all sites) based on the density of each species at each site and then averaging ranks across all sites by each factor level (i.e., rank of mean rank).

Species-specific differences in densities (fish•10^3 m^{-2}) of frequently observed fishes (observed at >20% of sites; 21 of 75 total species) were tested between habitat types, depth zones, relief levels, and complexity levels with generalized linear hurdle models (GLMs) in R (R Core Team, 2017) with the *a priori* significance level set at $\alpha = 0.05$. A GLM with a binomial distribution link function was used to test the effect of each factor and interaction terms on the presence/absence of each guild. A GLM with a gamma distribution link function was used to test the effect of each factor and interaction terms on the estimated density of each species.

A four-way PERMANOVA was computed to test the effects of reef type, depth, relief, and complexity on trophic structure (i.e., trophic guild-specific densities). The PERMDISP and SIMPER procedures also were applied to trophic guilds as described above for species-specific densities. Trophic guild was specified for each species based on diet data or inferences from morphological descriptions reported in previous studies (Supplementary Table 1; see Appendix A for full citations). Trophic guilds included herbivores that predominantly ingest benthic plant material; pelagic planktivores that occupy the water column and consume planktonic prey items; reef planktivores that directly utilize reef habitat for refuge but predominantly feed on planktonic invertebrates; large (≥200 mm TL) or small (<200 mm TL) demersal invertivores that sift or consume individual prey items in or on the benthos (i.e., sand or mud); large or small demersal browsers that consume epifaunal invertebrates on or associated with hard substrate surfaces; generalist carnivores that consume a wide variety of prey types (i.e, zooplankton, invertebrates, and fishes) from both pelagic and benthic habitats; and piscivores that consume predominantly fish prey.

Trophic guild-specific differences in density (fish•10^3 m^{-2}) were tested with the same statistical approach as described above for species-specific densities. Habitat type, depth zone, relief level, and complexity level were included in GLM hurdle models as explanatory variables with the *a priori* significant level set to $\alpha = 0.05$.

3. Results

Forty-seven reef sites were surveyed in 2017, with 23 being ARs and 24 being NRs (Table 1). Twenty-four sites were within the shallow depth stratum and 23 were within the deep stratum. Twenty-six sites were classified as having low relief and 21 as having high relief. Twenty-four sites were classified as having low complexity and 23 as having high complexity. Among all samples, 32,785 individual fish comprising 75 species from 34 families were identified; an additional 15,129 individuals were observed but could not be identified due to small size (<100 mm), distance from the camera, or turbidity. Individuals that could not be identified to species were excluded from the analyses except for difficult to distinguish Pomacentrids, which were aggregated and included in analyses. Here, Pomacentridae refers to *Chromis scotti*, *Stegastes adustus*, and *Stegastes fuscus* because they are difficult to distinguish in ROV survey videos.

Table 1
Number of video samples collected for each treatment for factors reef type (reef type (artificial, AR or natural, NR), depth (shallow, ≤35 m or deep, >35 m), relief (low, ≤2 m or high, >2 m), or complexity (low or high) at reef sites sampled in the northcentral Gulf of Mexico in 2017.

Depth	Relief	Complexity	Reef type	
			AR	NR
Shallow	Low	Low	6	2
Shallow	Low	High	2	4
Shallow	High	Low	3	2
Shallow	High	High	2	3
Deep	Low	Low	3	3
Deep	Low	High	2	4
Deep	High	Low	3	2
Deep	High	High	2	4

The mean (±SE) number of species was similar between ARs (13.2 ± 1.0) and NRs (13.3 ± 1.3), shallow (14.3 ± 1.2) and deep (12.2 ± 1.1) reefs, and between low- (13.7 ± 1.2) and high-relief (12.7 ± 1.1) reefs. Reefs with high complexity (15.7 ± 1.2) had nearly 5 more species on average compared to low complexity (11.0 ± 0.9) reefs. Fishery species comprised 7 of the 10 more frequently observed species among all reef sites, with *Lutjanus campechanus* (81%), *Rhomboplites aurorubens* (79%), *Haemulon aurolineatum* (62%), *Balistes capriscus* (60%), *Lutjanus griseus* (60%), *Pagrus pagrus* (55%), and *Seriola dumerili* (55%) observed at ≥50% of all reef sites (Table 2; Supplementary Table 2). Among these, *Rhomboplites aurorubens* and *Haemulon aurolineatum* were nearly always the most dense with each species having mean densities of several hundred individuals per 10^3 m^{-2}. Small demersal reef fishes (SDRFs) not targeted by fishers, such as *Chromis enchrysura*, *Stegastes leucostictus*, and Pomacentridae, also were frequently observed at reef sites. Transient pelagic fishes were rarely observed but occurred in dense aggregations when present (Table 3).

3.1. Community structure

Community structure was significantly different between reef types ($p < 0.001$), depths ($p < 0.001$), relief levels ($p = 0.002$), and complexity levels ($p = 0.046$); the interaction among reef type, depth, and relief ($p = 0.037$) also was significant. The PERMDISP procedure indicated that dispersion was significant for reef type ($p = 0.039$), but not for depth ($p = 0.130$), relief ($p = 0.406$), or complexity ($p = 0.944$). The mean (±SE) distance from centroid for ARs was 40.6 (±1.7) and 47.6 (±2.4) for NRs. Although significant in the PERMDISP procedure, a difference in dispersion between reef types was only weakly apparent in the non-metric MDS plot (Fig. 3A). Dispersion was not significant for the interaction among reef type, depth, and relief ($p = 0.604$). Clustering was apparent when sites were plotted by factor levels but separation was weak between levels of each factor (Fig. 3). SIMPER analyses indicated 14 species commonly contributed to at least 50% of dissimilarity between levels of main effects (Fig. 4A). The remaining 61 species each contributed <2.5%. A stacked barplot of proportional species composition among levels of the significant interaction among reef type, depth, and relief from PERMANOVA analysis indicates that the relative composition of 1) pelagic forage fish (*Decapterus* spp.) was less at reef sites in deep water or with high relief, 2) *Seriola dumerili* was greater at ARs with high relief, 3) *Haemulon aurolineatum* was greater at shallow reefs and was zero at low-relief NRs in deep water; 4) *Pagrus pagrus*, *Pristogenys alta*, *Chromis enchrysura*, and Pomacentridae was greater at NRs (Fig. 4B).

Community structure at reef sites by mean rank was consistently dominated by 6 fishery species, 3 small demersal reef fish (SDRFs), and the invasive *Pterois volitans* (Supplementary Table 3). These 10 species comprised the top 10 by mean rank in 90.0% of comparisons between

Table 2
Proportion of sites for each frequently observed species (i.e., prop. sites >0.20) and mean density [fish•10^3 m^{-2} (±SE)] by reef type (artificial, AR or natural, NR), depth (shallow, ≤35 m or deep, >35 m), relief (low, ≤2 m or high, >2 m), or complexity (low or high) at reef sites sampled in the northcentral Gulf of Mexico in 2017.

Species	Prop. sites	AR	NR	Shallow	Deep	Low relief	High relief	Low complexity	High complexity
Lutjanus campechanus	0.81	150.6 (36.2)	18.1 (7.6)	82.8 (27.5)	83.1 (30.9)	112.9 (31.8)	45.8 (21.4)	107.5 (28.2)	57.4 (29.3)
Rhomboplites aurorubens	0.79	906.2 (558.3)	287.5 (106.2)	889.2 (535.7)	278.4 (105.9)	452.9 (112.2)	760.4 (615.6)	451.9 (116.1)	734.7 (562.4)
Pterois volitans	0.74	63.7 (18.6)	6.75 (1.93)	29.4 (9.42)	40.1 (18.0)	52.8 (16.9)	12.1 (4.9)	45.7 (15.3)	23.0 (12.6)
Holacanthus bermudensis	0.66	8.27 (2.11)	2.10 (0.55)	4.73 (1.36)	5.52 (1.91)	5.83 (1.79)	4.23 (1.34)	5.54 (1.93)	4.68 (1.26)
Haemulon aurolineatum	0.62	583.4 (255.0)	271.6 (165.3)	734.0 (279.4)	100.9 (51.6)	602.5 (264.9)	203.4 (63.4)	436.6 (168.0)	411.3 (257.5)
Balistes capriscus	0.60	42.5 (13.9)	5.74 (2.02)	26.2 (12.2)	21.2 (8.2)	35.2 (12.1)	9.59 (5.75)	30.2 (12.2)	17.0 (7.9)
Lutjanus griseus	0.60	40.0 (10.1)	5.82 (3.58)	35.6 (9.9)	8.88 (4.24)	17.8 (5.5)	28.4 (11.0)	14.3 (5.2)	31.1 (10.3)
Pagrus pagrus	0.55	5.24 (2.51)	4.51 (1.10)	5.60 (2.02)	4.11 (1.77)	4.68 (1.59)	5.10 (2.29)	3.93 (1.66)	5.85 (2.13)
Seriola dumerili	0.55	44.5 (23.8)	4.03 (1.51)	36.4 (22.9)	10.7 (4.5)	11.6 (5.0)	39.0 (26.0)	11.8 (5.4)	36.4 (23.7)
Chromis enchrysura	0.40	6.52 (5.90)	9.51 (3.93)	4.95 (3.39)	11.3 (6.2)	11.9 (5.9)	3.29 (2.51)	13.2 (6.6)	2.65 (1.30)
Pomacentridae	0.36	33.0 (19.2)	77.9 (42.0)	98.0 (44.2)	12.1 (6.0)	76.0 (39.9)	31.1 (17.4)	27.0 (15.0)	86.2 (44.9)
Mycteroperca phenax	0.34	2.44 (0.80)	0.78 (0.29)	1.45 (0.50)	1.74 (0.72)	1.50 (0.54)	1.71 (0.71)	1.58 (0.53)	1.61 (0.70)
Rypticus maculatus	0.34	7.50 (2.51)	0.42 (0.25)	6.11 (2.42)	1.55 (0.81)	5.64 (2.26)	1.70 (0.88)	6.04 (2.43)	1.63 (0.81)
Stegastes leucostictus	0.34	5.00 (2.09)	3.01 (1.16)	5.27 (1.59)	2.65 (1.73)	4.36 (1.63)	3.52 (1.73)	3.84 (1.72)	4.14 (1.64)
Chaetodon ocellatus	0.30	4.26 (1.23)	0.44 (0.24)	2.02 (0.72)	2.61 (1.17)	2.37 (0.76)	2.24 (1.20)	2.65 (0.82)	1.95 (1.09)
Equetus lanceolatus	0.30	7.84 (4.76)	2.72 (1.57)	8.82 (4.69)	1.47 (0.83)	8.75 (4.34)	0.86 (0.56)	8.53 (4.71)	1.78 (0.84)
Pristigenys alta	0.30	0.00 (0.00)	4.92 (1.72)	1.83 (1.20)	3.22 (1.47)	2.43 (1.14)	2.61 (1.60)	2.31 (1.22)	2.72 (1.47)
Pareques umbrosus	0.28	8.44 (3.71)	2.35 (1.49)	7.17 (3.38)	3.41 (2.05)	8.58 (3.46)	1.31 (0.70)	9.07 (3.72)	1.43 (0.73)
Ptereleotris calliura	0.23	0.00 (0.00)	8.07 (3.38)	7.19 (3.42)	0.92 (0.59)	4.55 (2.75)	3.58 (2.26)	4.86 (2.98)	3.35 (2.07)
Canthigaster rostrata	0.21	1.10 (0.68)	0.45 (0.15)	0.70 (0.48)	0.84 (0.50)	0.71 (0.44)	0.83 (0.55)	0.70 (0.48)	0.84 (0.50)
Seriola rivoliana	0.21	6.68 (2.51)	0.26 (0.22)	4.50 (1.74)	2.26 (1.97)	1.73 (0.98)	5.47 (2.63)	4.52 (2.33)	2.23 (1.11)

Table 3
Mean density [fish 10^3 m^{-2} (±SE)] of each trophic guild by reef type (artificial, AR or natural, NR), depth (shallow, ≤35 m or deep (>35 m), relief (low, ≤2 m or high, >2 m), or complexity (low or high) at reef sites sampled in the north-central Gulf of Mexico in 2017. Trophic guilds are herbivore (H), pelagic planktivore (PP), reef planktivore (RP), large demersal invertivore (LDI), small demersal invertivore (SDI), large demersal browser (LDB), small demersal browser (SDB), generalist carnivore (GC), and piscivore (Pi). The number of species in each trophic guild is indicated in the second column.

Trophic guild	Species	AR	NR	Shallow	Deep	Low relief	High relief	Low complexity	High complexity
H	1	0.25 (0.25)	0.00 (0.00)	0.24 (0.24)	0.00 (0.00)	0.00 (0.00)	0.27 (0.27)	0.00 (0.00)	0.25 (0.25)
PP	2	1604.5 (1348.8)	255.1 (200.1)	1526.0 (1293.5)	278.4 (209.3)	1569.9 (1200.5)	105.2 (151.7)	438.4 (228.3)	1413.2 (1351.4)
RP	10	946.1 (559.0)	385.4 (135.0)	994.7 (538.3)	310.3 (112.7)	544.0 (134.7)	803.1 (615.9)	302.8 (72.7)	1032.3 (567.1)
LDI	10	50.1 (14.3)	10.9 (2.8)	33.8 (12.3)	26.2 (9.0)	41.0 (12.3)	16.5 (6.9)	30.0 (9.9)	30.1 (11.8)
SDI	10	616.7 (256.0)	292.1 (165.1)	778.9 (278.5)	108.7 (51.6)	642.6 (264.9)	213.6 (63.7)	307.3 (79.5)	600.9 (298.0)
LDB	6	9.6 (2.5)	2.8 (0.6)	5.7 (1.4)	6.6 (2.4)	7.2 (2.2)	4.8 (1.5)	6.3 (2.3)	6.0 (1.5)
SDB	6	10.4 (3.1)	5.4 (1.4)	8.3 (1.6)	7.3 (3.0)	7.8 (2.1)	7.8 (2.7)	7.7 (2.5)	7.9 (2.2)
GC	23	337.0 (55.4)	69.1 (29.8)	242.6 (54.7)	155.9 (47.5)	247.9 (48.8)	141.1 (53.5)	261.0 (55.0)	136.7 (45.3)
Pi	7	21.2 (12.6)	1.2 (0.3)	17.4 (12.2)	4.3 (1.3)	15.1 (11.2)	5.9 (1.9)	17.8 (12.1)	3.9 (1.4)

factor levels. *Rhomboplites aurorubens* had the highest mean rank regardless of factor level, while *Lutjanus campechanus* and *Pterois volitans* were always in the top 5 by rank. Notable exceptions were that 1) Pomacentridae were 7-ranks higher at NRs (3rd) than ARs (10th) and 17-ranks higher at reefs with high complexity (2nd) than low complexity (19th), 2) *Chromis enchrysura* were 18-ranks higher at NRs (4th) than ARs (22nd) and 8 ranks higher at deep (6th) than shallow (14th) reefs, 3) *Haemulon aurolineatum* was 8-ranks higher at shallow (2nd) than deep (10th) reefs, and 4) *Seriola dumerili* was 8-ranks higher at high-relief (3rd) than low-relief (11th) reefs.

3.1.1. Species-specific analyses

Sixteen of the 21 (76.2%) frequently observed fishes were present at much higher densities on ARs than NRs; 57.1% had higher densities at shallow reefs; 61.9% had higher densities at low-relief reefs; and 52.4% had higher densities at low-complexity reefs (Table 2). All eight frequently observed fishery species had higher densities at ARs than at NRs. Seven had higher densities at shallow reefs with only *Lutjanus campechanus* and *Mycteroperca phenax* having slightly higher densities at deeper sites. Five had higher densities at high- than at low-relief reefs and five had higher densities at low- than at high-complexity reefs. Specifically, *Lutjanus campechanus*, *Haemulon aurolineatum*, *Balistes capriscus*, *Chromis enchrysura*, Pomacentridae, *Rypticus maculatus*, *Equetues lanceolatus*, and *Pereques umbrosus* were much more dense (2–10-fold) at low-relief reefs. Only *Seriola dumerili* and *Seriola rivoliana* had higher densities (3-fold) at high-relief reefs. Invasive *Pterois volitans* density was 10 times higher at ARs; 36.4% higher at deep reefs; 4.4 times higher at low-relief reefs; and twice as high at low-complexity reefs. *Chromis enchrysura, Rypticus maculatus, Equetus lanceolatus, Pareques umbrosus* had much higher densities (between 2- and 5-fold) at low- than high-complexity reefs.

For the 21 frequently observed species, the binomial component of species-specific, GLM hurdle models indicated none of the four factors or their interaction terms had a significant effect on their presence/absence at reef sites ($p > 0.05$ for all tests). At sites where a species was present, the gamma component of hurdle models indicated densities of several species were significantly affected by interactions among main effects (Supplementary Tables 4a and b) including one or more two-way interactions among reef type, depth, relief, or complexity. Some species were significant for one or more three-way interactions. Among fishery species, *Lutjanus campechanus* density was just 5.0% of the mean ($p = 0.034$) at reefs with high relief and high complexity; *Balistes capriscus* density was 27.2 times greater ($p = 0.014$) at high-relief reefs in deeper water; *Seriola dumerili* density was just 1.0% of the mean

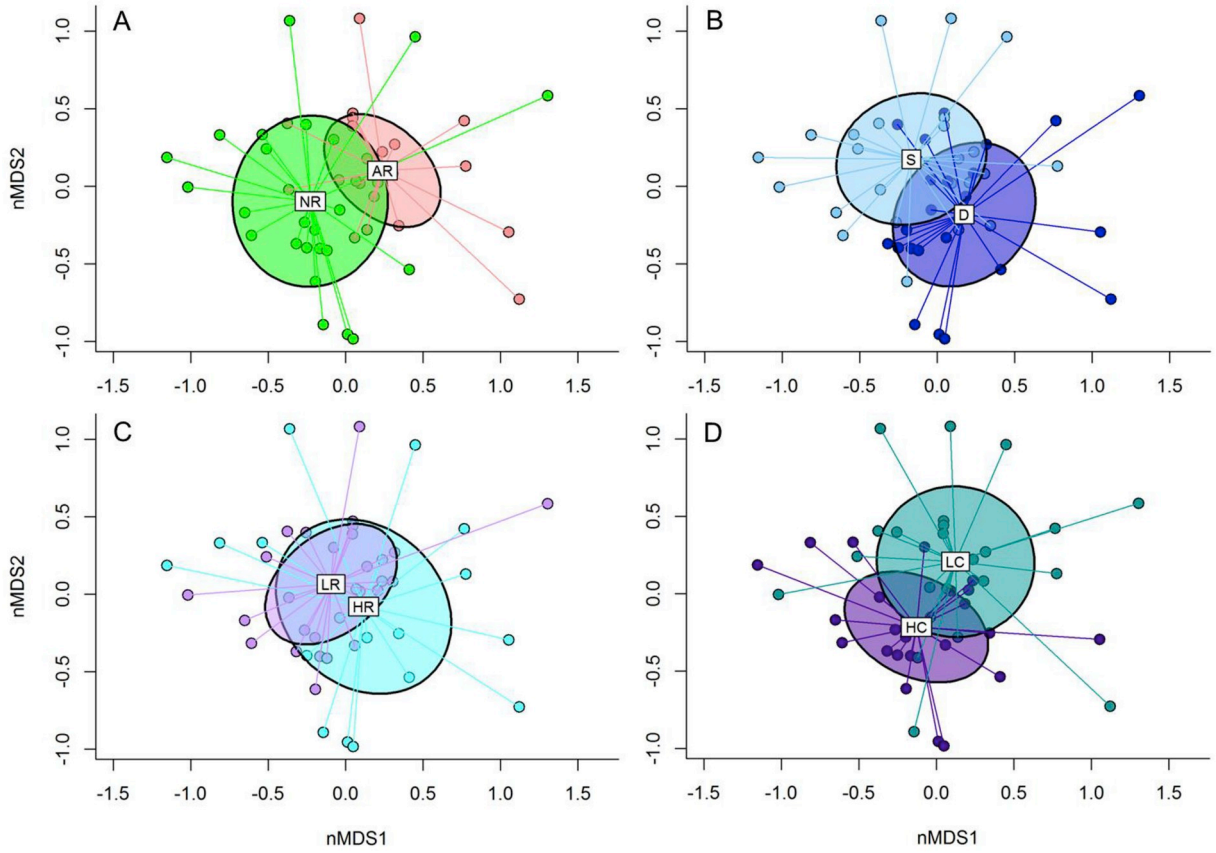

Fig. 3. Non-metric multidimensional scaling (nMDS) plots of Bray-Curtis dissimilarities (4th-root transformed densities [fish•10^3 m^{-2}]) by A) reef type (AR or NR), B) depth (shallow, ≤35 m or deep, >35 m), C) relief (low [LR], ≤2 m or high [HR}, >2 m), and D) complexity (low [LC] or high [HC]) at reef sites sampled in the northcentral GOM in 2017. Labels indicate group centroids and ellipsoids indicate values lying within 1 standard deviation from the group centroid.

($p = 0.029$) at natural reefs with high complexity. *Rhomboplites aurorubens* were extremely dense at natural reefs in deeper water with high relief and high complexity ($p = 0.001$). *Mycteroperca phenax* and *Seriola rivoliana* density was not significantly different at any factor level or for any interaction terms. Among SDRFs, *Holocanthus bermudensis* and *Canthigaster rostrata* were significant for multiple two-way interactions (Supplementary Table 4a) while no main effect significantly affected *Rypticus maculatus*, *Chaetodon ocellatus*, *Equeteus lanceolatus*, *Pristegenys alta*, *Pereques umbrosus*, or *Ptereoleotris calliura* density. Among the Pomacentrids, Pomacentridae were 76.4 times denser than the mean at natural reefs with high complexity ($p = 0.048$); *Stegastes leucostictus* density was 6.8 times higher at natural reefs with high complexity ($p = 0.112$) but only 4% of the mean at deep reefs with high complexity ($p = 0.045$); *Chromis enchrysura* density was 69.2 times higher than the mean at natural reefs with high relief ($p = 0.039$). Many SDRFs were not observed in all treatment combinations precluding tests of three-way interaction terms. Invasive *Pterois volitans* density was only 6% of the mean at natural reefs ($p = 0.031$) and <1.0% of the mean at deeper reefs with high relief and high complexity ($p = 0.035$).

3.2. Trophic structure

Trophic structure was significantly different between reef types (four-way PERMANOVA; $p < 0.001$) and depths ($p < 0.001$) but not between relief levels ($p = 0.164$) or complexity levels ($p = 0.546$). However, there was a significant interaction between relief and complexity ($p = 0.032$). The PERMDISP procedure indicated that dispersion was not significant for reef type ($p = 0.177$), relief ($p = 0.996$), or complexity ($p = 0.806$), but was significant for depth ($p = 0.027$). The mean (±SE) distance from the centroid for shallow depth was 19.3 (±1.8) and 24.9 (±1.5) for deep depth. A difference in dispersion between depth levels was not detectable upon visual inspection with a non-metric MDS plot. Dispersion was not significant for the interaction between relief and complexity ($p = 0.657$). Cluster analysis indicated that sites separated into three significant groupings (Fig. 5). The first group was comprised primarily of a subset of NRs in deep water, most of which had high relief, high complexity, or both (Fig. 5A, B). Within the second major grouping was a small cluster of ARs with high complexity (Fig. 5A, C). The remaining subset was comprised of more than half the total sites comprised of different combinations of relief and complexity treatments. SIMPER analyses, excluding herbivores and pelagic planktivores, indicated that small demersal invertivores, reef planktivores, and generalist carnivores contributed nearly 60% of the dissimilarity between reef types, depths, or the interaction between relief and complexity; small demersal invertivores contributed between 24.0 and 28.9% in each of the three comparisons. Piscivores, large demersal invertivores, and small demersal browsers each contributed between 9.0 and 11.6% to percent dissimilarity between factor levels or the interaction between relief and complexity (Fig. 6).

3.2.1. Trophic guild-specific analyses

The binomial component of trophic guild-specific GLM hurdle models indicated none of the four factors or their interactions had a significant effect on guild presence at reef sites ($p > 0.05$ for all tests). However, the gamma component of hurdle models indicated that densities of all trophic guilds, excluding herbivores and pelagic planktivores, were significantly affected by one or more factors or their interactions (Supplementary Tables 5a and b). Reef planktivore density was 13,248 times higher than the mean (i.e. intercept value) at deep

natural reefs with high relief and high complexity ($p = 0.002$). Densities of large ($p = 0.26$) or small demersal invertivores ($p = 0.005$) and small demersal browsers ($p = 0.049$) were 12.0, 5.0, and 5.0% of the mean at natural reefs, respectively. Large demersal browsers ($p = 0.020$) were 53.6 times denser and generalist carnivores ($p = 0.022$) were 45.5 times denser on natural reefs in deeper water with high relief. Piscivore densities decreased significantly ($p = 0.024$) at deeper reef sites to only 11.0% of the mean.

4. Discussion

Study results indicate that reef fish communities in the nGOM, currently, are likely best characterized as late seral communities at intermediate stages of progressive succession (Smith, 1976). This progressive succession appears to affect proportional composition and density without substitution and is unlikely to reach any dynamic equilibrium due to a combination of persistent anthropogenic and ecological factors. Regional diversity (i.e., the total number of unique species) is moderate to high while site-specific diversity is generally low with the same few species numerically dominant at most sites. Considerably richer and more diverse communities have been observed in the nGOM associated with unique bathymetric features (i.e., the Florida Middle Grounds or Flower Garden Banks) located in shallow mesophotic depths that can support tropical fish and corals species and are partially or fully protected from fishing (Dennis and Bright, 1988; Koenig et al., 2000; Gledhill, 2001). Decades of historical overfishing of top predators (SEDAR, 2017), piscivores (SEDAR, 2014a; SEDAR, 2014b), and meso-predators (SEDAR, 2015; SEDAR, 2018), invasion by the voracious generalist carnivore (*Pterois volitans*) beginning in 2009 (Dahl and Patterson, 2014), and the Deepwater Horizon oil spill in 2010 (Mendelssohn et al., 2012; Beyer et al., 2016; Etnoyer et al., 2016) likely have altered the composition of reef fish communities. Increasing

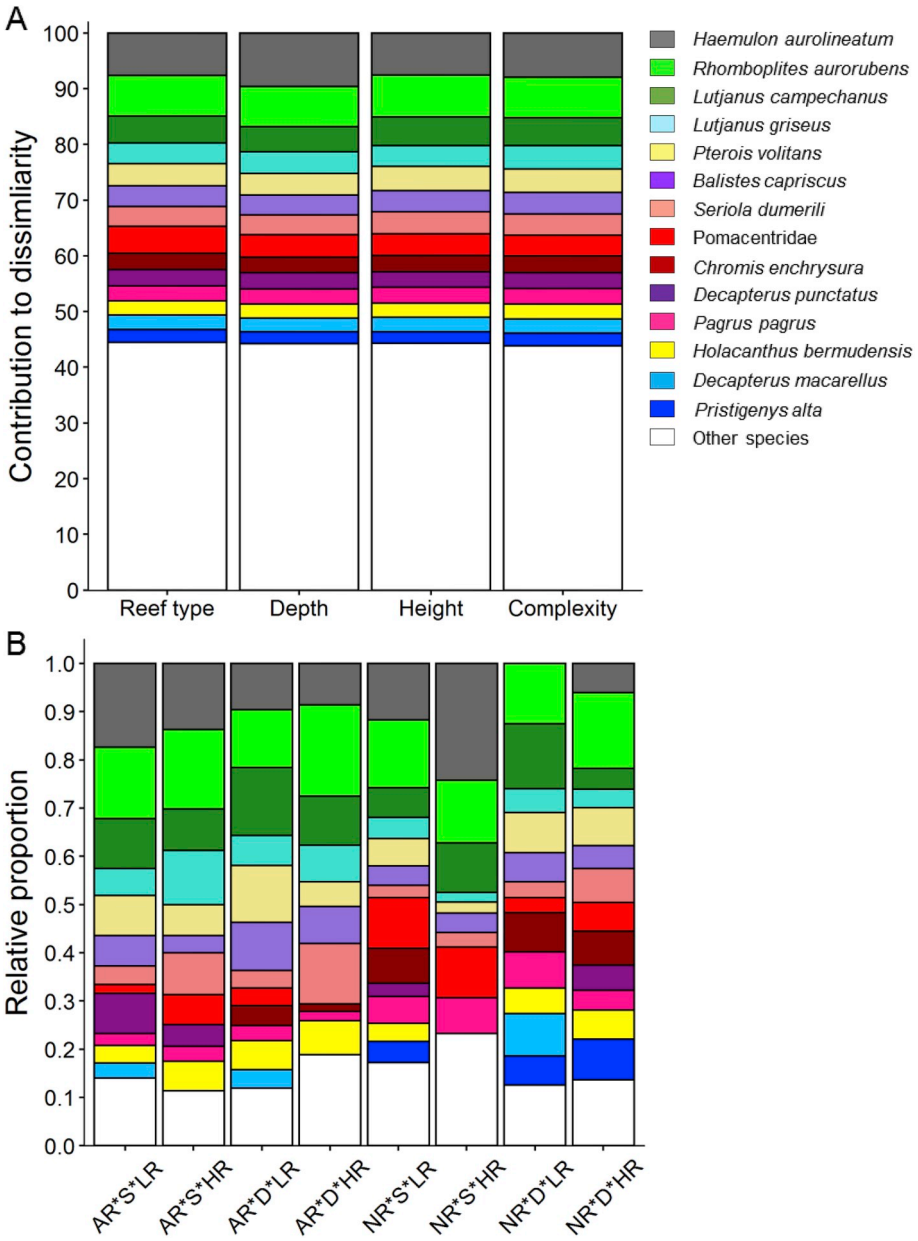

Fig. 4. Species-specific A) contribution to percent dissimilarity (SIMPER) by reef type, depth, relief, and complexity, and B) species-specific relative proportions by treatment interaction terms among reef types (AR or NR), depths [shallow ($S \leq 35$ m) or deep ($D > 35$ m)], and relief levels [low relief ($LR \leq 2$ m) or high relief ($HR > 2$ m)] at reef sites sampled in the northcentral GOM in 2017.

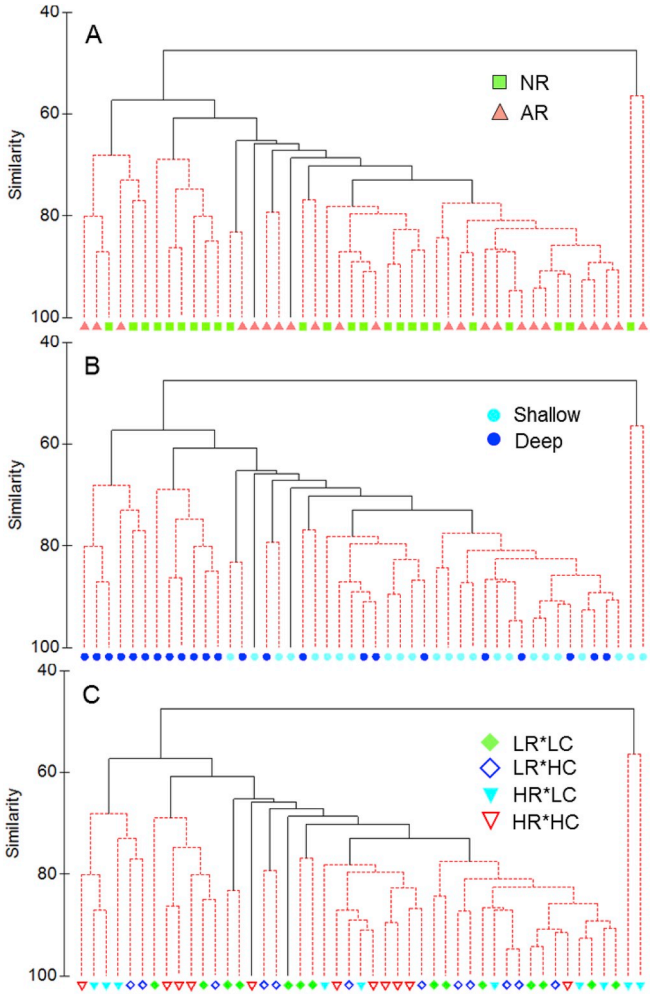

Fig. 5. Cluster dendrograms of trophic guilds (densities [fish•10^3 m^{-2}]) by A) reef type (AR or NR), B) depth (shallow, ≤35 m or deep, >35 m), or the interaction between relief (low [LR], ≤2 m or high [HR}, >2 m) and complexity (low [LC] or high [HC]) at reef sites sampled in the northcentral GOM in 2017. Dendrograms were constructed with Bray-Curtis dissimilarity matrices on group averaged, 4th-root-transformed densities. Solid vertical connections indicate significant differences in cluster groupings estimated with the SIMPROF procedure ($p \leq 0.05$) while red connections indicate non-significant differences ($p > 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

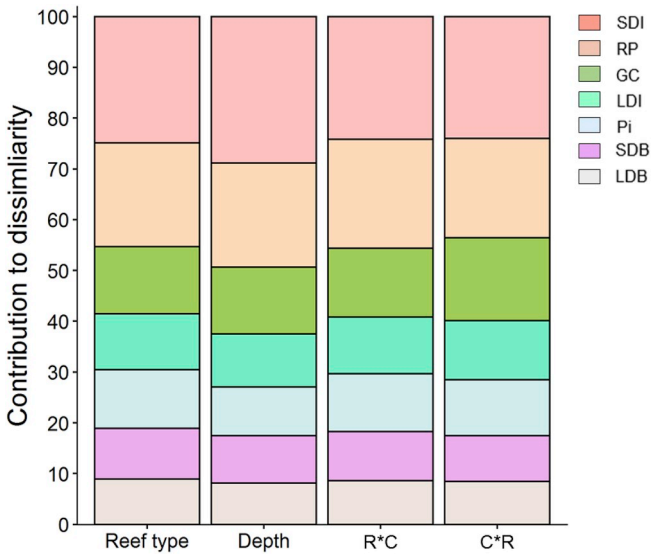

Fig. 6. Trophic guild-specific (4th root-transformed densities) contribution to percent dissimilarity (SIMPER) between reef type (AR or NR), depth (shallow, ≤35 m or deep, >35 m), or the interaction between relief (low, ≤2 m or high, >2 m relief) and complexity (low or high) and reef sites sampled in the northcentral GOM in 2017. In column three, relief is compared across levels of complexity (R*C) and complexity is compared across levels of relief (C*R) in column four. Legend abbreviations indicate small demersal invertivores (SDI), reef planktivores (RP), generalist carnivores (GC), large demersal invertivores (LDI), piscivores (Pi), small demersal browsers (SDB), or large demersal browsers (LDB).

temperatures due to climate change will continue warming coastal waters allowing more stenothermal sub-tropical species to expand northward (Fodrie et al., 2010).

Resource limitation (Sale, 1977; Hixon and Beets, 1989, 1993), competition (Sale, 1977; Carr et al., 2002; Almany, 2003), predation (Hixon and Beets, 1993; Forrester and Steele, 2000; Carr et al., 2002; Almany, 2003) and stochastic recruitment (Sale and Dybdahl, 1975; Sale, 1977; Hixon and Beets, 1993) all have been proposed as primary mechanisms regulating reef fish communities in the western Atlantic (Adams and Ebersole, 2009). Community structure at nGOM reef sites has been attributed to species-specific resource utilization, predator-prey interactions, and ontogenetic shifts in habitat requirements (Adams and Ebersole, 2009). Reef type and depth (Patterson et al., 2014), relief and complexity (Chandler et al., 1985), and overall complexity (Lingo and Szedlmayer, 2006; Dance et al., 2011) all have been separately identified as significant drivers of reef fish community structure among locally disconnected studies in the nGOM.

When we tested the effects of reef type, depth, relief, and complexity concomitantly, more nuanced relationships emerged. Relief and complexity, and to a lesser degree depth, clearly play a strong role in structuring reef communities in this region of the nGOM. Relief and complexity can provide both food and refuge for small, lower-level consumers as well as increase predation success for upper-level consumers. Reef type seems to disproportionately affect several fishery species withou altering densities of other species with similar trophic ecology. Moderate similarity among the majority of our study sites likely results from a combination of factors including generalist trophic ecology, variable states of habitat succession, and study design. We necessarily classified reef attributes into broad binary categories when in fact they reside on a continuum of depth, height, and complexity with mature ARs possibly approaching similar fouling communities compared to NRs. All four of the main effects we tested were significant drivers of community composition, but interactions among main effects resulted in order of magnitude density differences for many abundant species, especially those that rely directly on reef resources for refuge. Surprisingly, none of the factors we tested or their interactions significantly affected the presence of any species suggesting one or more additional variables likely control regional diversity.

The more frequent and numerically dominant reef fishes we observed were habitat generalists or fishes that exhibit ontogenetic shifts (Adams and Ebersole, 2009) with relatively high mobility and low site fidelity that are capable of inter-site movements on daily timescales and region-scale movement during their lifetime (McClellan and Cummings, 1997; Patterson et al., 2001; Afonso et al., 2009; Murie et al., 2013). Ontogenetic shifters occupy different habitats depending upon development, competitors, age, and resource availability (Adams and Ebersole, 2009). For example, red snapper, observed at >80% of sites in this study, settle onto unstructured sand or mud and shell rubble habitat, recruit to reef structures at approximately 1–2 years of age (100–200 mm TL), and may dissociate from structures entirely at older ages (Wells and Cowan, 2007; SEDAR, 2005). *Lutjanus campechanus* as well as *Seriola dumerili* have high intra-annual site fidelity but low inter-annual site fidelity with home ranges nearer 10s–100s of kilometers during their lifetime (Patterson et al., 2001; Murie et al., 2013).

Mobility and opportunistic feeding ecology allow habitat generalists to occupy a variety of habitat types differing in resource availability and quality to increase survival and productivity.

Densities of obligate reef fishes with low mobility and high site fidelity are likely strongly regulated by reef complexity, the strength of which our data indicate is multiplied by the interaction among reef characteristics. The mean multiplier for the interaction between habitat type and complexity for Pomacentridae was more than 10 times higher than any other interaction tested. Hixon and Beets (1993) concluded that resource availability affected local densities of SDRFs (e.g., Pomacentrids) competing for food and refuge, but that predators ultimately regulated maximum prey abundance. Sufficient larval supply and the storage effect sustain densities near saturation levels (Hixon and Beets, 1993; Hixon and Jones, 2005; Secor, 2007). Despite predator densities being relatively low in this region, complexity likely still directly reduces predation pressure on SDRFs by regulating the availability of size-specific refuges (Hixon and Beets, 1993; Hixon and Jones, 2005). The recently invaded *Pterois volitans* is a voracious predator of SDRFs that is exceptionally dense at ARs but also common at lower densities at NRs (Dahl and Patterson, 2014). Serranids are cryptic mesopredators with extremely large mouth gapes relative to body size that are gape limited by only the largest reef fishes, and Carangids are large transient reef fishes that often travel in schools. Either resident or transient predators can induce density-dependent predation when prey species exceed threshold levels (Hixon and Carr, 1997; Holbrook and Schmitt, 2002). Higher complexity also supports higher densities of demersal browsers or herbivores by increasing the surface area available to epiphytic algae and sessile invertebrates (Petraitis, 1990; Fuchs, 2013).

Complexity has a significant impact on reef fish community structure but can have bidirectional effects when a component part is examined (e.g., refuge size). We were unable to directly measure the number of refuges per habitat or mean refuge size due to the complexity of natural reef formations, but refuge size can regulate the relative proportions of predators and prey occupying a reef (Lindberg et al., 1990; Hixon and Beets, 1993; Gratwicke and Speight, 2005b). Larger refuges provide hiding places for large predators that are still vulnerable to predation by top predators while smaller refuges provide shelter for prey species from mesopredators. The subset of NRs we examined are primarily either relic biogenic limestone reefs built by hermatypic corals and other calcifying invertebrates, or sandstone rocks of relic shorelines exposed during past geologic periods or erupted at the benthic surface atop salt diapirs (Thompson et al., 1999; Hine et al., 2008). Thus, some high-complexity NRs comprised of sandstone may provide primarily large refuges while those comprised of biogenic limestone in shallow waters may provide primarily small refuge spaces ideally occupied by SDRFs. Reef-specific morphology in either case is dependent upon the current colonial invertebrate community (primarily octocorals) present, the degree of reef sedimentation from fluvial and storm-induced deposition, and prior geologic-scale events. In addition, some obligate reef fishes (e.g., *Stegastes leucostictus* and *Holacanthus bermudensis*) exhibit strong territoriality, which may dull our ability to detect affinities for different reef morphologies in field experiments for these and other species with similar behavior (Hourigan et al., 1989). When conspecifics are dense, aggressive individuals exclude more timid conspecifics from low-vulnerability habitats to ecotone margins more exposed to predators (Holbrook and Schmitt, 2002). Territoriality could explain the relatively high frequency but consistently low densities observed for some obligate reef fishes with larger body sizes concomitant with low predator abundance (Robertson, 1996).

Our results suggest that non-reef resource utilization strategies facilitate the numerical dominance of a few species at most reef sites. Diet studies indicate that many of the more frequently observed and abundant reef fishes (e.g., Lutjanids or Haemulids) are habitat generalists that do not utilize reef-derived food resources (Nelson and Bortone, 1996; McCawley and Cowan, 2007; Adams and Ebersole, 2009). Rather, structured habitats serve as predation refugia from which reef fishes radiate to forage (Lindberg et al., 1990; Nelson and Bortone, 1996; Campbell et al., 2011). For example, *Rhomboplites aurorubens*, the most abundant fish across all factor levels, form relatively large aggregations as juveniles or adults and feed on zooplankton above and away from reefs (Grimes, 1979; Sedberry and Cuellar, 1993). *Pristigenys alta*, which were only observed at NRs in this study, are directly reliant upon reef crevices for shelter but also feed primarily on zooplankton (Bryan et al., 2013). Other fishes that were numerically dominant among study reefs (e.g., *Lutjanus campechanus*, *Haemulon aurolineatum*, or *Pagrus pagrus*) consume primarily benthic invertebrates and occasional fishes from sediments surrounding reef structures (Manooch, 1977; McCawley and Cowan, 2007; Wells et al., 2008). Radiative foraging behaviors concomitant with high site fidelity can form benthic halos depleted of invertebrate resources around reef sites (Davis et al., 1982; Lindberg et al., 1990; Langlois et al., 2005; Campbell et al., 2011). Habitat generalists (e.g., Lutjanids and Haemulids) and mobile mesopredators (e.g., Carangids) may utilize a spatial mosaic of reef sites (both artificial and natural) or follow directional structure (e.g., relic shorelines and escarpments) to avoid resource limitation along reef/sand ecotones (Adams and Ebersole, 2009). Significantly higher densities of Carangids at high-relief reefs may result from increased predation success in a more 3-dimensional foraging arena compared to a more 2-dimensional arena at low-relief structures.

Additional factors likely play a significant role in structuring reef fish communities at larger spatial scales (i.e., Gulf-wide). At similar latitudes in the nGOM as our study, Ajemian et al. (2015) observed reef fish communities at various large ARs that were numerically dominated by *Lutjanus campechanus* but also by *Bodianus rufus* (Family: Labridae) and *Epinephelus adscensionis* (Family: Serranidae) as well as 28 additional species that were not observed in our study. The same is true for results presented by Streich et al. (2017) upon comparing reef fish communities at large ARs (i.e., oil rig platforms) and nearby NRs. Results of reef fish studies in the eastern GOM indicate dominant species along the Florida Panhandle (e.g., *Lutjanus campechanus*, *Rhomboplites aurorubens*, and *Haemulon aurolineatum*) are reduced in abundance along the West Florida Shelf while congeners with stricter thermal tolerances increase in density (Bohnsack, 1983; Koenig et al., 2000; Kuffner et al., 2007; Dupont, 2009). Thermal tolerances play a strong role in limiting the persistent northward range of tropical congeners of species we observed in the northcentral nGOM (Smith, 1976; Miller and Richards, 1980).

Significantly higher abundances of facultative and obligate reef fishes at ARs in otherwise unstructured habitats are frequently perceived as evidence for increased population production. We observed much higher mean densities of several reef fishes at ARs compared to NRs, especially Lutjanids, Carangids, and some Serranids, which comprise the primary reef-fish fisheries in the nGOM. Careful examination of fishery species' feeding ecology, condition, and life history components (Lindberg et al., 2006; McCawley and Cowan, 2007) indicate that ARs may simply concentrate juveniles and young adults without increasing productivity because AR resources are relatively sparse and population bottlenecks occur in other habitats (e.g., sargassum or shell rubble) prior to recruitment to complex reef structures (Cowan et al., 2011). Smaller structures maximize the edge-to-habitat area ratio to facilitate radiative foraging behavior for fishes consuming non-reef prey while also providing refuge. Natural reefs diffuse reef fish biomass over a much larger area making fishing activities less efficient (Karnauskas et al., 2017). Despite the abundance of ARs that now exist in the nGOM and densities up to 20 times higher for some fishery species, natural banks, ridges, and diapirs still far exceed the total benthic footprint of ARs and may support more than 90% of the reproductive output for some reef fish populations in the eastern nGOM due to age-specific fecundity and ontogenetic shifts in habitat utilization (Karnauskas et al., 2017). Concentrating biomass at known locations via AR deployments can negatively impact fishing opportunities by dramatically increasing catchability, and hence, fishing mortality, which may far exceed increases in survival or growth of reef fishes attributable to ARs (Cowan

et al., 2011; Karnauskas et al., 2017).

Non-fishery SDRFs also may not experience population-level benefits from ARs. Of the frequently observed fishes in our study, *Pristigenys alta* (observed only at natural reef sites), *Chromis enchrysura*, and Pomacentridae were denser at natural reefs suggesting that ARs, especially those with low-complexity, may not provide sufficient food or refuge from predators. Both *Holacanthus bermudensis* and *Stegastes leucostictus* were denser at ARs but both are territorial and were observed only at low densities. The potential proportional contribution to population abundance by ARs increases when fish densities are much lower at NRs, but population level increases in production are likely modest considering the dramatically different benthic footprints of ARs vs NRs in the nGOM, even for obligate reef fishes that depend on 3-dimensional structure throughout ontogeny. High densities of invasive *Pterois volitans* at ARs may transform isolated ARs from potential refuge oases into strong sinks for SDRFs and juveniles of some fishery species (Dahl and Patterson, 2014).

Many ARs deployed in the nGOM to enhance fishing opportunities consist of single simple geometric shapes with little complexity prior to colonization by invertebrate fouling communities. Fishery managers seeking to maximize the ecological impacts of ARs, beyond increased fishing opportunities, should focus on reef designs that maximize structural complexity and benthic footprint. Complex ARs should contain structural refuges appropriately sized for SDRFs while also supporting the growth of epiphytic invertebrates that provide additional food and refuge. Spatially expansive ARs, such as debris fields or multiples of the same structures deployed together may dilute fish over a larger area and possibly decrease catchability. The depth of AR deployment also will affect the proportional abundance of some reef-dependent species.

This study provides a robust assessment of the reef fishes currently occupying mesophotic reefs in the central nGOM and identifies specific habitat characteristics that affect community and trophic structure. Our data can help facilitate species-specific vulnerability assessments to current (e.g., climate change) and future ecosystem-level threats (e.g., oil spills). Disconnected sub-region and region-scale studies have been conducted throughout the last several decades to characterize reef fish communities across a variety of habitats in the eastern and western nGOM. However, environmental drivers and anthropogenic stressors are not continuous in time, space, or magnitude. The GOM, like other LMEs, supports heterogeneous complexes of reef communities among sub-regions due to differing productivity, geological, temperature, and hydrodynamic regimes. This complexity necessitates region-scale studies to assess the recent impacts from invasive species and pollution and to monitor distributional and morphological shifts in reef communities due to climate change (Scavia et al., 2002; Coleman and Koenig, 2010; Fodrie et al., 2010). Our data provide a (shifted) baseline to help assess and monitor the recovery of reef fish communities from invasive lionfish or oil spill impacts as well as future impacts of warming, acidifying waters due to climate change.

Declaration of competing interest

None.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106423.

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