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Fish assemblages associated with red grouper pits at Pulley Ridge, a mesophotic reef in the Gulf of Mexico

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Abstract—Red grouper (*Epinephelus morio*) modify their habitat by excavating sediment to expose rocky pits, providing structurally complex habitat for many fish species. Surveys conducted with remotely operated vehicles from 2012 through 2015 were used to characterize fish assemblages associated with grouper pits at Pulley Ridge, a mesophotic coral ecosystem and habitat area of particular concern in the Gulf of Mexico, and to examine whether invasive species of lionfish (*Pterois* spp.) have had an effect on these assemblages. Overall, 208 grouper pits were examined, and 66 fish species were associated with them. Fish assemblages were compared by using several factors but were considered to be significantly different only on the basis of the presence or absence of predator species in their pit (no predators, lionfish only, red grouper only, or both lionfish and red grouper). The data do not indicate a negative effect from lionfish. Abundances of most species were higher in grouper pits that had lionfish, and species diversity was higher in grouper pits with a predator (lionfish, red grouper, or both). These results may indicate that grouper pits are a favorable habitat for both lionfish and native fish species or that the presence of lionfish is too recent to have caused changes to fish community structure.

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The red grouper (*Epinephelus morio*) has been harvested in the United States since the 1880s and is currently the most common grouper species landed in both commercial and recreational fisheries of the Gulf of Mexico (Fisheries Statistics Division, National Marine Fisheries Service, Annual Commercial Landing Statistics, website, and Saltwater Recreational Data and Statistics, website). Like other grouper species, the red grouper is a slow growing, late maturing, relatively stationary, and long lived fish (Moe[1]; Jory and Iversen[2]). Adult red grouper inhabit the deeper waters (>70 m) of the shelf edge and have been known to modify their habitat by excavating sediment to expose rocky depressions (or pits) on the seafloor in areas where vertical relief is not already present (Coleman et al., 2010). Red grouper use these pits as their home territories (Scanlon et al., 2005). These excavations increase the architectural complexity of the habitat, attracting many reef-associated species and providing shelter for juveniles of some economically important species and, thereby, increasing biodiversity (Coleman et al., 2010). By excavating the sediments, red grouper act as "ecological engineers" and may play an important role in influencing community dynamics (Jones et al., 1994; Coleman and Williams, 2002; Coleman et al., 2010).

Grouper pits have been described for 2 marine protected areas (MPAs) in the northeastern Gulf of Mexico: Madison-Swanson and Steamboat Lumps MPAs, which were established in 2000 on the shelf break (at

[1] Moe, M. A., Jr. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. 10, 95 p.

[2] Jory, D. E., and E. S. Iversen. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida)—black, red, and Nassau groupers, 21 p. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.110). U.S. Army Corps Eng., TR EL-82-4. [Available from website.]

depths of 50–120 m) to alleviate fishing pressure on aggregations of gag (*Mycteroperca microlepis*). Grouper pits at Steamboat Lumps consist of carbonate rocks that have been scoured out from a thick veneer of carbonate-derived sediment. The pits are on average 5–6 m in diameter but can become as large as 25 m in diameter and 1–2 m deep with a density of about 250 pits/km^2 (Scanlon et al., 2005; Coleman et al., 2010; Wall et al., 2011). Pits in the Madison-Swanson MPA differ in their level of relief; some have a thin veneer of carbonate-derived sediments and some have more relief (Coleman et al., 2010).

Our study area was at Pulley Ridge, a mesophotic coral ecosystem (MCE) in the northeastern Gulf of Mexico, which has large populations of red grouper and a high density of grouper pits. This geological feature is a carbonate ridge that extends for nearly 300 km along the southwestern shelf of Florida and lies about 250 km west of the Florida coastline (Hine et al., 2008). The southern end of Pulley Ridge supports an MCE at depths of 60–100 m and covers an area of ~600 km^2 (Fig. 1; Jarrett et al., 2005; Cross et al.[3]; USGS[4]; Hine et al., 2008; Reed, 2016). Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and their associated communities, and Pulley Ridge is the deepest MCE on the U.S. continental shelf (Halley et al.[5]). The hard-bottom substrate along this ridge consists of rock and coral pavements and cemented conglomerates of carbonate rubble and cobble rock (5–15 cm in diameter) that provide habitat for hermatypic corals (primarily *Agaricia* spp., great star coral [*Montastraea cavernosa*], and *Madracis* spp.), macroalgae, sponges, and a large variety of species of tropical fish (Phillips et al., 1990; Halley et al.[5]; Reed, 2016). The Pulley Ridge Habitat Area of Particular Concern (HAPC) was established in 2005 by the Gulf of Mexico Fishery Management Council[6] to provide protection from bottom longlines and trawls. Hook-and-line fishing, however, is still allowed. The established HAPC provides protection for 348 km^2, an area that is roughly half the total MCE area (Reed, 2016).

Structural complexity has often been shown to positively influence abundance and diversity of fish species (McClanahan, 1994; Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005; Harter et al., 2009). Most of Pulley Ridge is a low relief, low rugosity, rock and rubble habitat. The highest densities of fish reside on 2 biologically derived habitat features that provide more structural complexity: mounds of rock rubble and cobble created by sand tilefish (*Malacanthus plumieri*) and grouper pits (Halley et al.[7]). The grouper pits are large enough (8–15 m in diameter and 1–2 m deep) to be visible in high-resolution bathymetric images collected with a multibeam sonar during a research cruise in September 2011 (NOAA[8]), and up to 340 pits/km^2 are visible in those images. Approximately 90 species of fish, both shallow-water and deepwater species, have been observed on Pulley Ridge (Jaap et al., 2015). The fish communities of Pulley Ridge have been characterized previously, but communities associated with the grouper pits specifically have not.

Species of lionfish (*Pterois* spp.) first were discovered on Pulley Ridge during submersible dives in 2010 (Reed and Rogers[9]) when 6 fish were observed. Since then, exponential increases in the abundance of this population of lionfish have been observed (Andradi-Brown et al., 2016). It is unknown at this time whether red lionfish (*P. volitans*), devil firefish (*P. miles*), or both species exist at Pulley Ridge. At this time, positive identification can be achieved only through genetic analysis; therefore, lionfish were identified only to genus level for this study. The invasion of lionfish is regarded as one of the most successful colonizations of a marine species ever documented (Albins and Hixon, 2008; Green and Côte, 2009; Albins, 2013). Lionfish first were recorded in waters of the Atlantic Ocean in the mid-1980s, but their range has expanded to include the Gulf of Mexico, Caribbean, and much of the tropical and subtropical western Atlantic Ocean (Schofield, 2009, 2010). Over the years, densities of lionfish in the western Atlantic Ocean have expanded rapidly to the point that they are nearly 5 times more abundant in the invaded range (Green and Côte, 2009) than in the Pacific Ocean (Kulbicki et al., 2012). High individual growth and reproductive rates (Morris and Whitfield, 2009) have contributed to the rapid increase of the population in the western Atlantic Ocean. Many stud-

[3] Cross, V., D. C. Twichell, R. B. Halley, K. T. Ciembronowicz, B. D. Jarrett, E. S. Hammar-Klose, A. C. Hine, S. D. Locker, and D. F. Naar. 2005. GIS compilation of data collected from the Pulley Ridge deep coral reef region. U.S. Geol. Surv. Open-File Rep. 2005-1089. [Available from website.]

[4] USGS (U.S. Geological Survey). 2005. Recently discovered reef is deepest known off continental U.S. ScienceDaily, 5 January 2005. [Internet press release available from website.]

[5] Halley, R. B., V. E. Garrison, K. T. Ciembronowicz, R. Edwards, W. C. Jaap, G. Mead, S. Earle, A. C. Hine, B. Jarret, S. D. Locker, et al. 2003. Pulley Ridge—The United States' deepest coral reef? *In* U.S. Geological Survey Greater Everglades Science Program: 2002 biennial report. U. S. Geol. Surv. OFR-03-54, 153–154 p. [Available from website.]

[6] Gulf of Mexico Fishery Management Council (GMFMC). 2005. Essential Fish Habitat Amendment 3. Addressing essential fish habitat requirements, habitat areas of particular concern, and the adverse effects of fishing on fishery management plans of the Gulf of Mexico.

[7] Halley, R., G. P. Dennis, D. Weaver, and F. Coleman. Halley, R., G. P. Dennis, D. Weaver, and F. Coleman. 2005. Part II: characterization of the Pulley Ridge coral and fish fauna. Final report to the National Oceanic and Atmospheric Administration Coral Reef Conservation Grant Program, 25 p. [Available from website.]

[8] NOAA. 2011. Multibeam sonar bathymetry data collected aboard Nancy Foster (NF-11-09-CIOERT). NOAA National Centers for Environmental Information. [Available from website.]

[9] Reed, J. K., and S. Rogers. 2011. Final cruise report. Florida Shelf-Edge Expedition (FLoSEE), Deepwater Horizon oil spill response: survey of deepwater and mesophotic reef ecosystems in the eastern Gulf of Mexico and southeastern Florida. R/V Seward Johnson and Johnson-Sea-Link submersible, July 9–August 9, 2010, 16 p. [Available from website.]

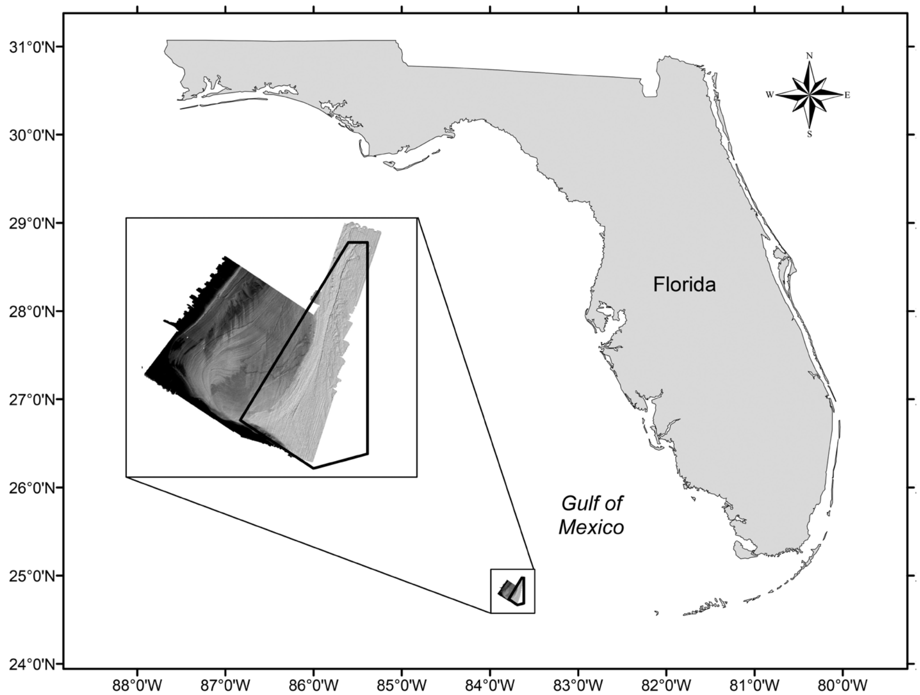

Figure 1

Map of the Pulley Ridge mesophotic coral ecosystem off southwestern Florida in the Gulf of Mexico where video surveys were conducted with a remotely operated vehicle during 2012–2015. The polygon outlined in black represents the Pulley Ridge Habitat Area of Particular Concern. The extent of the survey area includes the entire area of available multibeam bathymetric imagery.

ies have revealed deleterious effects of the invasion of lionfish on abundances and species richness of native fish through predation and competition (Albins and Hixon, 2008; Green et al., 2012; Albins, 2013). In addition, studies of MCEs in the Bahamas found that predation by lionfish on herbivorous fish has caused a shift in the benthic fauna, and an increase in the proportion of algae to the proportion of corals (Lesser and Slattery, 2011).

Because the grouper pits of Pulley Ridge have not been characterized previously, particularly since the invasion of lionfish, our objectives for this study were 1) to quantify and characterize fish populations associated with grouper pits at Pulley Ridge, 2) to estimate the spatial distribution and abundance of key economically and ecologically important reef fish species, and 3) to examine the effect of lionfish on the abundance and composition of fish communities of the grouper pits.

Materials and methods

Data collection

Information on the fish community in the grouper pits was collected annually from 2012 to 2015 by using underwater video cameras attached to remotely operated vehicles (ROVs) that were deployed from the RV *F. G. Walton Smith*. Video surveys were conducted with 2 different ROVs: the *Phantom S-2* in 2012–2013 and the *Mohawk* in 2014–2015. Both vehicles are operated by the Undersea Vehicles Program of the University of North Carolina at Wilmington. To keep the ROV near the seafloor during dives, a "down weight" (145 kg) was tethered to its umbilical cable at a distance of 25–30 m behind the ROV. The configuration of the down weight allowed the ROV to traverse just above the seafloor (<1 m) at a mean speed-over-ground of approximately 0.13 m/s (range: 0.13 to 0.28 m/s). The precise location of the ROV was recorded constantly throughout each dive with a tracking system linked to the GPS of the RV *F. G. Walton Smith*.

The *Phantom* ROV was equipped with a standard-definition Sony[10] color video camera (Sony Corp., Tokyo, Japan) with more than 460 lines of resolution, and the *Mohawk* ROV had a Mini Zeus II high-definition video camera (Insite Pacific Inc., Solana Beach, CA). Both cameras provided continuous video data recorded on external hard drives. On both ROVs, the camera typically was angled down ~30° to capture the view both

[10]Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

near to and far from the horizon in video recordings of fish aggregations and habitat. An on-screen display system recorded and superimposed time, date, ROV heading (direction), and ROV depth on the video taken with the cameras. The ROVs also had high-resolution digital cameras that captured still images of fish and habitats within the study area. The still cameras were mounted on the ROV in a fixed, downward-looking orientation for images of habitat cover. Both cameras were equipped with parallel lasers (10 cm) to calculate scale. Two 250-W halogen lights (DeepSea Power & Light, San Diego, CA) were mounted on top of the ROV tilt platform and provided illumination for the video cameras on the *Phantom*, and the *Mohawk* ROV had two 3700-lm SeaLite Sphere 3100 LED lights (DeepSea Power & Light). Water clarity and natural light, however, usually allowed visibility in excess of 20 m. When available, an SBE 39 temperature and depth recorder (Sea-Bird Scientific, Bellevue, WA) was attached to the ROV for each dive.

A statistically rigorous sampling protocol was used to select the ROV survey sites at Pulley Ridge. In ArcGIS, vers. 10.1 (Esri, Redlands, CA), a grid of blocks, each 1×1 km, was overlaid on maps created with multibeam bathymetric imagery collected by NOAA[7] (Fig. 1). Blocks were selected randomly to be surveyed quantitatively by the ROV over the 4 years, and the pooling of blocks for selection targeted both the Pulley Ridge HAPC and areas adjacent to the HAPC that appeared to be mesophotic habitat from the bathymetric maps. Areas outside the HAPC had been mapped previously, but the bathymetric maps have not yet been verified by direct observations, or ground-truth; therefore, areas interpreted as hard-bottom habitat from the bathymetric data were used in the selection of blocks. Once a block had been examined, it was not resampled in subsequent years. Each dive of the ROV lasted approximately 3–4 h during daylight hours and covered an average distance of 1.85 km (standard error [SE] 0.11). The direction of each dive within a block was selected haphazardly on the basis of a flip of a coin and the maneuverability of the ship, which is affected by wind and current, but the direction was not altered to target grouper pits.

Video reading

All fish were counted and identified in each encountered grouper pit, including species that were both inside the pit and swimming in the water column above (1–3 m) the pit. Individual fish were identified to the lowest taxonomic level possible, and fish counts for each taxon were made by using a tally system. Still images of single frames of video were used to identify and count fish when multiple species were present and when areas had high fish abundance. If confident identifications could not be made, individuals were recorded as *unknown*. Random segments of video were analyzed by a second reader to confirm identification of fish and accuracy of the primary reader's counts. Counts for large schools of fish (>100 individuals) were estimated by counting a group of 25 fish and then extrapolating that count for the size of the entire school. To avoid recounting fish, unique color patterns, body markings, and attraction behaviors (i.e., schooling of fish around the ROV) were noted. Fish abundances were recorded for each taxon observed in every grouper pit. Because pits were of relatively similar sizes, averaging ~10 m in diameter (as measured from high-resolution, multibeam bathymetric imagery) and 1–2 m in depth, fish abundance per pit, rather than density, was used. Coleman et al. (2010) found no relationship between pit diameter and either fish density or species abundance in the Madison-Swanson and Steamboat Lumps MPAs in the northeastern Gulf of Mexico.

Analyses of multivariate fish communities

Multivariate analyses were conducted by using PRIMER, vers. 6 (PRIMER-E, Auckland, New Zealand) to compare fish communities in the grouper pits. Each grouper pit was defined and characterized by the following 4 factors: year, predator presence or absence, region, and HAPC. Year indicated the year the grouper pit was sampled: 2012–2015 (Fig. 2A). Red grouper and lionfish are the 2 top-level predators that inhabit the grouper pits. To test the effect of predator presence or absence on community structure, grouper pits were categorized as 1) having either no predators (no lionfish or red grouper), 2) lionfish only, 3) red grouper only, or 4) both (red grouper and lionfish present) (Fig. 2B). Although in some cases on shallow reefs lionfish have been observed to move more than 1 km (Akins et al., 2014; Tamburello and Côté, 2015), both lionfish and red grouper are known for their site fidelity (Coleman et al., 2010; Jud and Layman, 2012; Bachelor et al., 2015). Coleman et al. (2010) examined the movement patterns of red grouper in pits specifically and found that they exhibit high site fidelity, remaining in the same pit for long periods of time (>1 year). Other predators around the grouper pits, such as other grouper species and species of snapper, are more roving predators. The region factor indicated the location of the grouper pits in relation to the geological features of the Pulley Ridge MCE, primarily on the basis of bathymetric maps. Four geological regions were used to categorize the location of each grouper pit: main ridge, off main ridge (area east of the main ridge), central basin, and west ridge (Fig. 2C). The HAPC factor indicated whether the pit was located inside or outside the HAPC.

Four multivariate routines in PRIMER were employed to examine fish communities by using the factors described previously. They were nonmetric multidimensional scaling (MDS), analysis of similarity (ANOSIM), similarity percentages (SIMPER), and biodiversity indices (DIVERSE) routines. For these analyses, taxa that composed less than 1% of the total abundance were removed to minimize the disproportionate effect they can have on the data. Data were averaged by factor and fourth-root transformed—a calculation

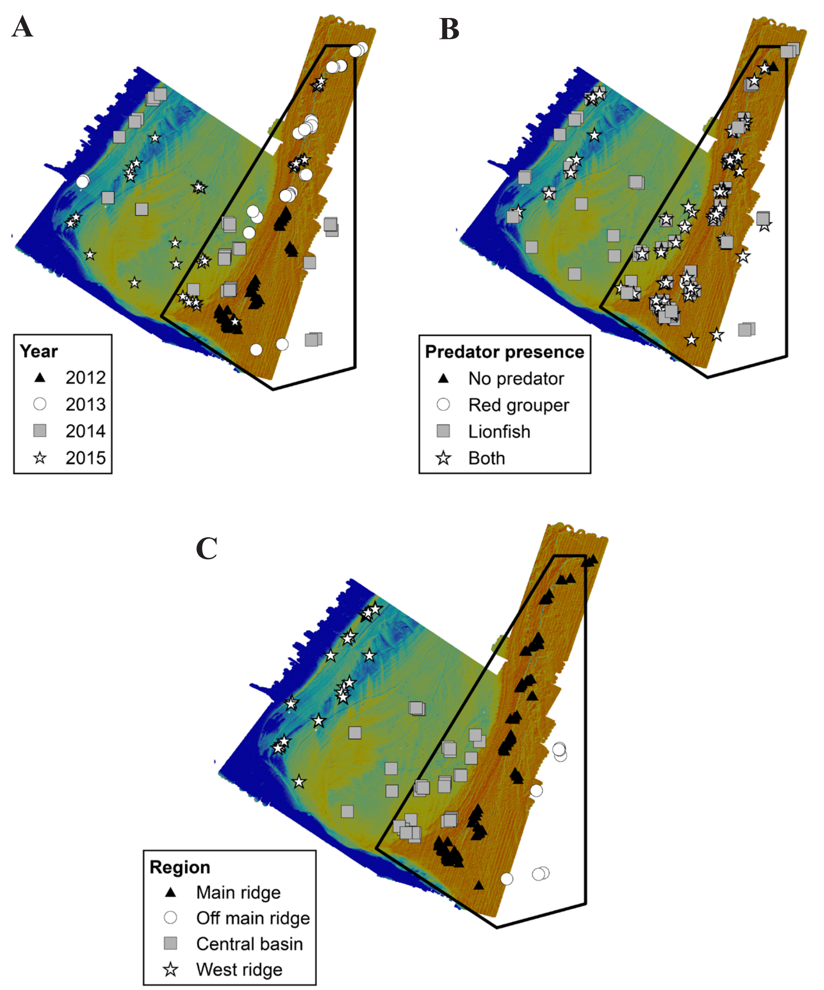

Figure 2

Locations of each grouper pit surveyed during 2012–2015 in the Gulf of Mexico, characterized by 3 of the factors used to compare fish assemblages at pits: (**A**) year, (**B**) predator presence, and (**C**) region. The polygon outlined in black represents the Pulley Ridge Habitat Area of Particular Concern, which is located off southwestern Florida. Predator presence or absence categories were no predator, red grouper (*Epinephelus morio*) only, species of lionfish (*Pterois* spp.) only, or both predators.

that "down-weighs" the dominance of highly abundant species, allowing species with intermediate density to exert some influence on the calculation of similarity (Clarke and Warwick, 2001).

An MDS routine based on Bray–Curtis similarity coefficients and a dendrogram with group-average linking were created to depict the results of a concurrent similarities profile (SIMPROF routine in PRIMER). The MDS routine is an ordination technique in which points that are located closer together in multivariate space are considered more similar than points further away. The stress values shown in MDS plots reflect the accuracy of the representation of community structure; lower stress values indicate that the plots are increasingly representative of the community structure. Stress values less than 0.20 generally indicate that plots provide an accurate representation of the data rather than that the points have been placed arbitrarily in the 2-dimensional ordination space.

We also tested for differences in community structure among pits with one-way ANOSIM tests based on the Bray-Curtis similarity coefficients. Significant differences among groups were defined in our study when $P \leq 0.05$, but for those pairwise tests that showed significant difference, we further examined the ANOSIM R-statistic. Unlike the P-value, the R-statistic reflects the absolute difference in community structure between treatments (i.e., it reflects the size of the effect) (Clarke et al., 2006). The R-statistic typically ranges from 0 to 1, with values closer to 1 representing more significant separation among groups and values closer to 0 representing no difference among groups. It is possible to obtain a significant P-value with an R-statistic that is very low when there are many replicates at each site, and obtaining a significant P-value in such a case would indicate little biologically significant separation among groups (Clarke, 1993). Negative R-values denote unusual situations where replicates among groups are more similar than within a group. Analysis of similarity percentages was then used to determine which species contributed to the dissimilarities between the group pairs.

Biodiversity indices derived with the DIVERSE routine were compared among grouper pits for each factor. Parameters examined included total number, diversity, and evenness of species in the community. The Shannon-Weiner function (H') was used to estimate pit diversity as $\Sigma_i\, p_i \log(p_i)$, where p_i is the proportion of the total count arising from the ith species. Pielou's evenness was estimated as $H'/\log(S)$, where S is the total number of taxa at a pit (Pielou, 1977).

Analyses of univariate fish abundance

Fish associated with grouper pits were divided into 3 categories: small fish, schooling fish, and large fish. This classification was needed because several of the species (primarily the economically important species)

Table 1

Summary information from video surveys conducted with a remotely operated vehicle during 2012–2015 at the Pulley Ridge mesophotic coral ecosystem off southwestern Florida in the Gulf of Mexico. N/A indicates that information was not available for that year.

Year	No. of 1-km² blocks surveyed	Average distance surveyed (km)	No. of grouper pits surveyed	Dates of survey	Depth range (m)	Bottom temperature range (°C)
2012	10	35.2	80	14–25 Aug	62.8–75.5	N/A
2013	15	29.4	41	12–27 Aug	60.3–93.9	N/A
2014	17	23.8	35	14–28 Aug	63.1–86.1	18.1–29.2
2015	28	33.4	52	23 Aug–2 Sept	59.3–105.5	19.0–22.52

were not abundant enough to examine individually. For all analyses, the replicate was each grouper pit, and average abundances (with standard errors) for each factor were calculated and compared. Significant differences existed when $P \leq 0.05$.

The small fish group consisted of taxa of small, benthic fish that typically reside inside the pit to use the structural complexity it offers. Taxa in the small fish category were cardinalfish (*Apogon* spp.); damselfish (*Chromis* spp.); small sea basses (Serranidae), including anthiids (Anthiinae); wrasses (*Halichoeres* spp.); and parrotfish (Labridae). Not only do these species use the grouper pits in the same manner, but they are all possible prey of lionfish and red grouper. Abundances of small fish were $\log_e$ transformed to correct for normality and then tested with one-way analysis of variance (ANOVA) to examine the effects of year, predator presence or absence, region, and HAPC. Categories for each factor were the same as the multivariate analyses: year was 2012–2015; predator presence or absence was either no predator, lionfish only, red grouper only, or both; region was main ridge, off main ridge, central basin, or west ridge; and HAPC was either inside or outside the protected area.

Taxa in the schooling fish category hover just above a grouper pit and usually travel in schools of greater than 50 individuals. This group included the striped grunt (*Haemulon striatum*), the school bass (*Schultzea beta*), and bonnetmouths (Haemulidae). Because of the nature of the abundance data for the schooling group (large variances among pits) and because transformations did not correct for normality, nonparametric Kruskal–Wallis tests were used to test for effects of year, predator presence, region, and HAPC on the abundances of taxa in the schooling group.

The final category, large fish, consisted of the larger taxa, most of which are managed by the Gulf of Mexico Fishery Management Council. This group included grunts (*Haemulon* spp.), except for the striped grunt; snapper (*Lutjanus* spp.); grouper (*Mycteroperca* spp., *Epinephelus* spp., and the graysby, *Cephalopholis cruentata*), except for the red grouper; triggerfish (*Balistes* spp.); and the hogfish (*Lachnolaimus maximus*). Again, transformations did not correct for non-normality this time because of low abundances; therefore, nonparametric Kruskal–Wallis tests were used to test the effects of the 4 factors (year, predator presence, region, and HAPC) on the abundance of taxa in the large fish group.

Results

In August of each year between 2012 and 2015, 70 random blocks (each 1 km²) were surveyed over the entire Pulley Ridge MCE region (Table 1). Within those blocks, 208 grouper pits were encountered and analyzed. The number of grouper pits observed by year was 80 in 2012, 41 in 2013, 35 in 2014, and 52 in 2015. The average distance surveyed per year was 30.5 km (SE 2.5). The temperature range was 18.1–29.2°C in 2014 and 19.0–22.5°C in 2015; however, these data were not available for 2012 and 2013 because a conductivity, temperature, and depth profiler was not on the ROV during those years. Depths sampled were slightly shallower in 2012 because dives that year were conducted primarily on the main ridge, which is shallower than the other regions. The central basin and west ridge areas of the Pulley Ridge MCE are slightly deeper (10–30 m) and were sampled during the remaining years of the surveys (Fig. 2).

Grouper pits were distributed throughout the sampling region. Their locations are shown in Figure 2 by year, region, predator presence, and HAPC. In general, all the regions surveyed have very similar habitat, except the off main ridge region, which is east of the main ridge and is a predominately soft-bottom substrate mixed with rock rubble and cobble. The other regions (main ridge, central basin, and west ridge) all have low relief (0–1 m) and a substrate consisting primarily of rock pavement (probably old, dead coral plates), and rock rubble and cobble (5–20 cm rock), or a combination of the latter 2 substrate types.

Bathymetric maps show grouper pits 8–15 m in diameter, 1–2 m deep, and evenly spaced about 100 m apart over much of the area. Up to 340 grouper pits were visible in a single 1-km² block on high-resolution bathymetric maps of main Pulley Ridge (NOAA[7]).

Table 2

Annual mean abundances of all taxa, observed during video surveys conducted with a remotely operated vehicle at Pulley Ridge, in the Gulf of Mexico, from 2012 through 2015. The overall mean is the average of the 4 annual values for each taxon. Taxa are listed in order from highest to lowest overall mean. Commercially or recreationally harvested species are noted in bold.

Scientific name	2012	2013	2014	2015	Overall mean
Haemulidae	124.09	4.05	0.00	0.00	32.04
Haemulon striatum	0.00	64.86	21.77	12.15	24.70
Schultzea beta	0.00	13.51	32.17	33.00	19.67
Apogon spp.	0.63	31.24	5.40	32.73	17.50
Chromis scotti	9.74	2.46	0.97	26.25	9.85
Pterois volitans	3.06	4.70	13.97	6.65	7.10
Hemanthias vivanus	0.00	0.00	26.37	0.00	6.59
Chromis enchrysura	2.50	7.35	10.51	2.46	5.71
Serranidae	0.05	21.62	0.00	0.00	5.42
Chromis spp.	2.73	4.68	0.00	7.10	3.62
Chromis insolata	2.48	2.41	4.63	4.17	3.42
Anthiinae	7.13	4.05	0.49	1.92	3.40
Apogon affinis	0.00	0.00	13.43	0.00	3.36
Coranthias tenuis	0.25	0.00	0.11	11.54	2.98
Apogon maculatus	4.44	2.97	0.71	0.00	2.03
Holocentrus spp.	0.50	3.65	2.34	1.02	1.88
Bodianus pulchellus	0.43	0.38	1.14	1.10	0.76
Chromis cyanea	1.81	0.68	0.17	0.31	0.74
Chaetodon sedentarius	0.35	0.73	0.71	0.58	0.59
Equetus lanceolatus	0.00	0.24	1.97	0.04	0.56
Centropyge argi	0.28	0.57	0.17	0.87	0.47
Canthigaster rostrata	0.08	0.03	1.29	0.31	0.42
Epinephelus morio	0.38	0.49	0.46	0.35	0.42
Holacanthus tricolor	0.38	0.16	0.26	0.46	0.31
Serranus tortugarum	0.06	0.03	0.00	1.15	0.31
Mycteroperca phenax	0.44	0.05	0.23	0.52	0.31
Sparisoma atomarium	0.13	0.00	0.49	0.27	0.22
Liopropoma eukrines	0.03	0.19	0.23	0.37	0.20
Holacanthus bermudensis	0.19	0.11	0.31	0.10	0.18
Chaetodon ocellatus	0.00	0.11	0.23	0.29	0.16
Stegastes partitus	0.06	0.14	0.00	0.38	0.15
Pronotogrammus martinicensis	0.00	0.16	0.26	0.13	0.14
Apogon pseudomaculatus	0.00	0.14	0.20	0.08	0.10
Halichoeres spp.	0.08	0.00	0.06	0.25	0.10
***Lutjanus* spp.**	0.01	0.00	0.20	0.15	0.09

Table Continued

These pits represent the only areas of Pulley Ridge that provide a diversity of structural habitat. Whereas most of Pulley Ridge is relatively flat and consists of rubble and pavement and little rugosity, the grouper pits provide moderate relief (1–2 m), slopes of 5–30°, and high-rugosity habitat. Rugosity here is defined as a degree of ruggedness of the rock bottom in relation to the size of rock ledges, holes, and crevices, which tend to provide the most structurally complex habitat for reef fish. The grouper pits provide habitat for a large variety and density of small reef fish, and the exposed rock provides habitat for sessile benthic biota. Although rugosity of the grouper pits was not measured quantitatively, it differed visually only for those grouper pits that were not actively being maintained by a predator. These abandoned pits tended to be filled with sediment and lack exposed rock ledges.

Overall, 66 fish taxa were observed in the grouper pits of Pulley Ridge, 16 of which are managed species (Table 2). Schooling species, such as bonnetmouths and the striped grunt, had the highest overall mean abundances (84.40 individuals/pit [SE 25.30]), but the species that composed the schooling category varied among years. Bonnetmouths dominated in 2012, but the striped grunt and the school bass were more abundant during 2013–2015. Of the small, benthic fish that

Table 2 *Continued*

Scientific name	2012	2013	2014	2015	Overall mean
Holacanthus ciliaris	0.08	0.05	0.11	0.12	0.09
Cephalopholis cruentata	0.14	0.00	0.09	0.08	0.08
Holocentrus adscensionis	0.11	0.11	0.00	0.00	0.06
Seriola rivoliana	0.03	0.08	0.09	0.00	0.05
Halichoeres bathyphilus	0.00	0.00	0.14	0.04	0.05
Muraenidae	0.01	0.05	0.03	0.08	0.04
Pomacanthus paru	0.09	0.00	0.03	0.04	0.04
Rypticus saponaceus	0.10	0.03	0.00	0.02	0.04
Mycteroperca interstitialis	0.11	0.03	0.00	0.00	0.03
Mycteroperca bonaci	0.06	0.00	0.00	0.08	0.03
Pseudupeneus maculatus	0.03	0.00	0.11	0.00	0.03
Acanthurus spp.	0.00	0.03	0.09	0.02	0.03
Pomacanthus arcuatus	0.00	0.05	0.03	0.04	0.03
Haemulon album	0.11	0.00	0.00	0.00	0.03
Gymnothorax moringa	0.03	0.00	0.09	0.00	0.03
Myripristis jacobus	0.10	0.00	0.00	0.00	0.03
Aulostomus maculatus	0.01	0.00	0.03	0.04	0.02
Epinephelus adscensionis	0.01	0.00	0.00	0.06	0.02
Balistes vetula	0.01	0.03	0.03	0.00	0.02
Epinephelus guttatus	0.03	0.00	0.00	0.04	0.02
Haemulon melanurum	0.00	0.05	0.00	0.00	0.01
Lutjanus analis	0.05	0.00	0.00	0.00	0.01
Priacanthus arenatus	0.00	0.03	0.00	0.02	0.01
Seriola dumerili	0.01	0.00	0.03	0.00	0.01
Lachnolaimus maximus	0.00	0.00	0.00	0.04	0.01
***Seriola* spp.**	0.00	0.00	0.00	0.04	0.01
Acanthurus coeruleus	0.00	0.00	0.03	0.00	0.01
Lutjanus buccanella	0.00	0.00	0.03	0.00	0.01
Lutjanus campechanus	0.00	0.00	0.03	0.00	0.01
Lutjanus griseus	0.00	0.00	0.03	0.00	0.01
Monacanthus tuckeri	0.00	0.00	0.03	0.00	0.01
Opsanus spp.	0.00	0.00	0.03	0.00	0.01
Serranus phoebe	0.00	0.00	0.03	0.00	0.01
Epinephelus itajara	0.00	0.03	0.00	0.00	0.01
Haemulon spp.	0.00	0.03	0.00	0.00	0.01
***Balistes* spp.**	0.03	0.00	0.00	0.00	0.01
Neoniphon marianus	0.03	0.00	0.00	0.00	0.01
Balistes capriscus	0.00	0.00	0.00	0.02	0.00
Paranthias furcifer	0.00	0.00	0.00	0.02	0.00
Serranus annularis	0.00	0.00	0.00	0.02	0.00
Mycteroperca venenosa	0.01	0.00	0.00	0.00	0.00
Scarus coelestinus	0.01	0.00	0.00	0.00	0.00

used the grouper pits, cardinalfish, damselfish, and anthiids were the most abundant taxa (mean: 54.70 individuals/pit [SE 6.70]). The red grouper and scamp (*Mycteroperca phenax*) were the most abundant economically important species (mean: 0.40 individuals/pit [SE 0.04] for red grouper and 0.35 individuals/pit [SE 0.07] for scamp). Average abundance of unidentifiable fish was 13.91 individuals/pit (SE 3.60).

The percentage of grouper pits with red grouper in them was 37.5% in 2012, 46.3% in 2013, 45.7% in 2014, and 34.6% in 2015—proportions that were not significantly different (one-way ANOVA: P=0.61). There were never multiple red groupers in any one pit, and they were distributed evenly inside and outside the HAPC, as well as across the various regions. Frequency of occurrence for red grouper was 40.6% inside and 35.1% outside the HAPC, proportions that were not significantly different (one-way ANOVA: P=0.54). Their frequency of occurrence was 40.4% on the main ridge, 37.5% at off main ridge, 37.5% in the central basin, and 44% on the west ridge. These values were also not significantly different (one-way ANOVA: P=0.97). Of red grouper that could be measured from the lasers mounted on the ROV, total length ranged from 50 to 80 cm (average: 60 cm).

In contrast, lionfish were observed in 72.5% of grou-

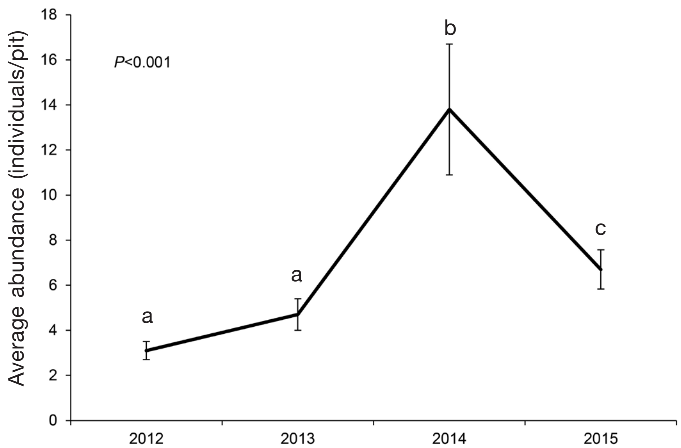

Figure 3

Average abundance of lionfish (*Pterois volitans* or *P. miles*) measured as number of individuals by year from surveys conducted from 2012 through 2015 at Pulley Ridge off southwestern Florida. The *P*-value is given for the results from one-way ANOVA. Statistically significant differences are noted with different letters (a–c); for years with the same letter, the difference is not significant. Error bars indicate standard errors of the mean.

per pits in 2012, 73.2% in 2013, 91.4% in 2014, and 86.5% in 2015. Although the maximum number of lionfish observed in a single pit was 74, the average abundance was 6.10 individuals/pit (SE 0.60), and the average abundance increased significantly over time ($P<0.0001$) (Fig. 3). Abundance of lionfish throughout the sampling area and presence of red grouper are displayed in Figure 4. Both species were distributed throughout the region, but the highest abundances of lionfish were located primarily outside the HAPC on the west ridge as well as a few places along the main ridge inside the HAPC.

Analyses of multivariate fish communities

Fish species composition associated with grouper pits was not significantly different for year, region, or HAPC factors. It did, however, differ depending on the predator species present (R-statistic=0.402, $P<0.01$). Three significantly different groups resulted from the SIMPROF test ($P< 0.05$), indicated by the letters on the MDS plot (Fig. 5). Grouper pits with lionfish only and with both predators formed one group, which meant that their fish assemblages were not significantly different from one another. Grouper pits with red grouper only formed their own group, as did those with no predators, which meant that their fish assemblages were significantly different from all other groups. The groups clustered together in this fashion at 80% similarity—a result that meant that the species composition of grouper pits with lionfish only and with both predators was 80% similar. Pairwise tests with the SIMPER routine indicated that the primary species responsible for the groups clustering in this way were cardinalfish and 3 damselfish species, including the sunshinefish (*Chromis insolata*), the purple reeffish (*Chromis scotti*), and the yellowtail reeffish (*Chromis enchrysura*). These species, as well as several others, including the scamp, striped grunt, and school bass, had higher abundances in grouper pits with either both predators or lionfish only than in grouper pits with no predators or red grouper only. Because the scamp was the most abundant economically important species observed (with the exception of red grouper), we needed to test the potential effect this species, as a predator, could have on fish assemblages in grouper pits through predation. The results of tests with the ANOSIM routine support the assertion that the presence of scamp did not affect fish assemblages of the grouper pits (R-statistic=0.169).

Species diversity and evenness did not differ considerably by HAPC or region but were different by year and predator presence (Table 3). All sampling years had similar species di-

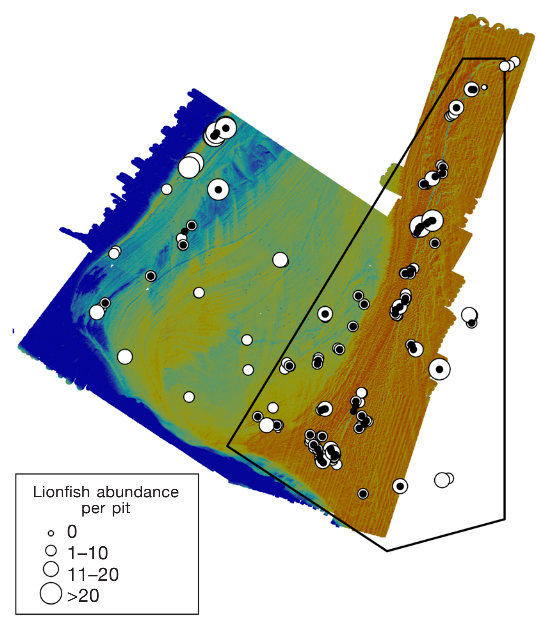

Figure 4

Average abundance of lionfish (*Pterois volitans* or *P. miles*) measured as number of individuals per grouper pit, for each pit surveyed during 2012–2015 off southwestern Florida. The size of the white circles indicates the level of abundance. Small black circles indicate the presence of a red grouper (*Epinephelus morio*). The polygon outlined in black represents the Habitat Area of Particular Concern at Pulley Ridge.

Figure 5

Plot of nonmetric multidimensional scaling ordination, derived from the Bray–Curtis similarity matrix constructed by using fourth-root transformed fish abundances averaged for each predator presence or absence category: no predator; red grouper (*Epinephelus morio*) only; species of lionfish (*Pterois* spp.) only; or both predators. Groups of fish assemblages surveyed at grouper pits during 2012–2015 off southwestern Florida are shown at 80% similarity. The closer 2 groups are in space, the more similar they are to each other. The letters (a–c) above the group symbols represent the results of the test with the SIMPROF routine in PRIMER software, and statistically different fish assemblage groups are indicated by different letters.

versity and evenness, with the exception of 2012, when those values were lower than those of other years. The lower species diversity in 2012 may have been observed because only the main ridge was sampled in that year. Species diversity and evenness were very similar for grouper pits with both predators, lionfish only, and red grouper only but were considerably lower for pits with no predators. In contrast, the highest number of species was observed in 2012 (again, this observation of a higher number of species may have occurred because only the main ridge was sampled in 2012), in grouper pits with either lionfish only or with both predators, inside the HAPC, and on the main ridge.

Analyses of univariate fish abundance

Average abundances of small fish associated with grouper pits were significantly different among years and predator groups (Fig. 6). Abundances significantly increased from 2012 to 2015 ($P<0.0001$) and species were more abundant in grouper pits with a predator present ($P=0.006$). Average abundances of small fish were not significantly different among regions or HAPC groups ($P>0.05$). In contrast, average abundances of schooling fish were not significantly different for any of the factors analyzed ($P>0.05$). Average abundances of large fish associated with the grouper pits were significantly different only among predator groups, where higher abundances were observed in grouper pits with either red grouper only or with both predators ($P<0.001$; Fig. 7). As with the multivariate analyses, we tested whether presence of scamp had an effect on abundances of

Table 3

Biodiversity indices for fish communities observed during video surveys conducted with a remotely operated vehicle at the Pulley Ridge mesophotic coral ecosystem in the Gulf of Mexico. Values are shown for each factor: year; predator presence; inside the Pulley Ridge Habitat Area of Particular Concern (HAPC) (area protected from fishing) and outside the HAPC (unprotected area); and the region of Pulley Ridge. *S*=total number of species; *H'*=Shannon-Wiener function of species diversity; *J'*=Pielou's evenness.

	S	*H'*	*J'*
Year			
2012	50	1.15	0.29
2013	41	2.09	0.56
2014	46	2.33	0.61
2015	43	2.26	0.60
Predator			
No predator	32	0.64	0.18
Red grouper only	24	2.10	0.66
Lionfish only	64	2.56	0.62
Both predators	56	2.48	0.62
HAPC			
Inside	65	2.38	0.57
Outside	42	2.36	0.63
Pulley Ridge			
Main ridge	61	2.05	0.50
Central basin	43	2.16	0.57
West ridge	40	2.26	0.61
Off main ridge	25	1.98	0.61

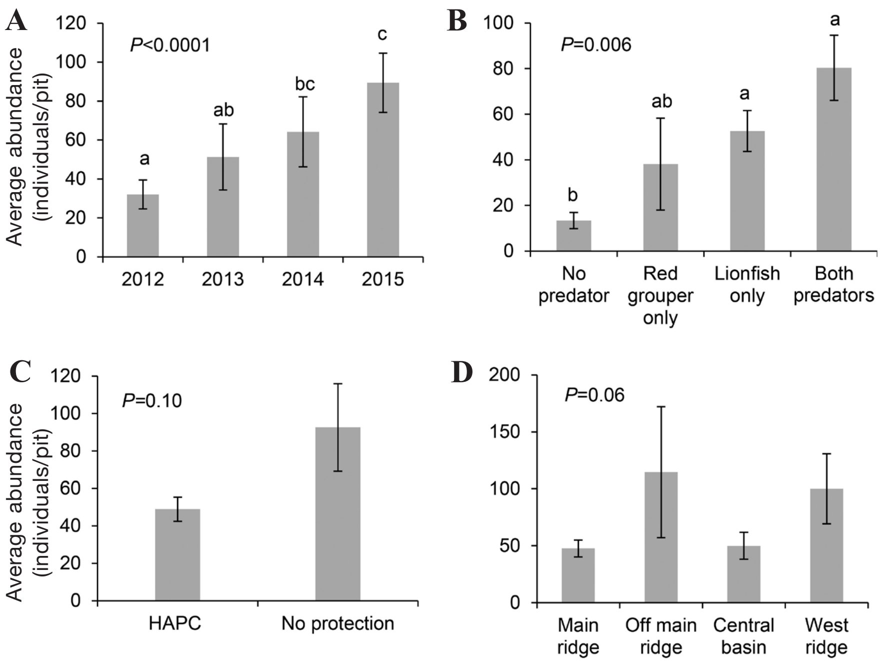

Figure 6

Average abundance measured as number of individuals of small benthic fish, including cardinalfish (*Apogon* spp.), damselfish (*Chromis* spp.), small sea basses (Serranidae), wrasses (*Halichoeres* spp.), and parrotfish (Labridae), associated with grouper pits surveyed during 2012–2015 off southwestern Florida, shown by the factor used to compare fish assemblages at pits: (**A**) year, (**B**) predator presence or absence, (**C**) inside or outside Pulley Ridge Habitat Area of Particular Concern (HAPC), and (**D**) region. Predators included the red grouper (*Epinephelus morio*) and species of lionfish (*Pterois* spp.). *P*-values are given for the results from one-way analysis of variance. Statistically significant differences are noted with different letters (a–c). Error bars indicate standard errors of the mean.

small and schooling fish through predation, possibly confounding other results observed. The results of tests with one-way ANOVA indicate that the presence of scamp did not have an effect on average abundances of either small fish (P=0.442) or schooling fish (P=0.244).

Discussion

Grouper pits inhabited by red grouper were observed to have greater species diversity and fish abundances compared with the levels observed at pits not inhabited by red grouper. These higher levels likely occurred because pits with red grouper are actively maintained, with the resident grouper of a pit using its fins and mouth to keep the pit scoured down to the rock ledges. The structural complexity of a pit remains intact, providing habitat for other fish species. Once a pit loses its grouper (to fishing capture in fisheries or for another reason), the pit begins to fill in with sediment, and the exposed ledges are covered. Average abundances of both small, benthic species and larger, managed species were significantly higher in pits with a red grouper present than in those with no predator. Some of the most abundant taxa in pits with red grouper present were the striped grunt, bonnetmouths, the school bass, cardinalfish, damselfish, and anthiids. Coleman et al. (2010) also observed higher species diversity in actively maintained grouper pits in the Steamboat Lumps and Madison-Swanson MPAs, which are 358 km north of Pulley Ridge. They found the most common species observed in those pits were the yellowtail reeffish, tomtate (*Haemulon aurolineatum*), the vermilion snapper (*Rhomboplites aurorubens*), the roughtongue bass (*Pronotogrammus martinicensis*), and a scad (*Decapterus* sp.).

An unusual observation from this study is the lack of a negative effect from lionfish on fish assemblages in the grouper pits that were analyzed. Most studies that have examined the effect of the invasion of lionfish on native fish species have been conducted in shallow water and have reported that lionfish adversely affect indigenous fish species (Albins and Hixon, 2008, 2013). In a study that is analogous to our work and

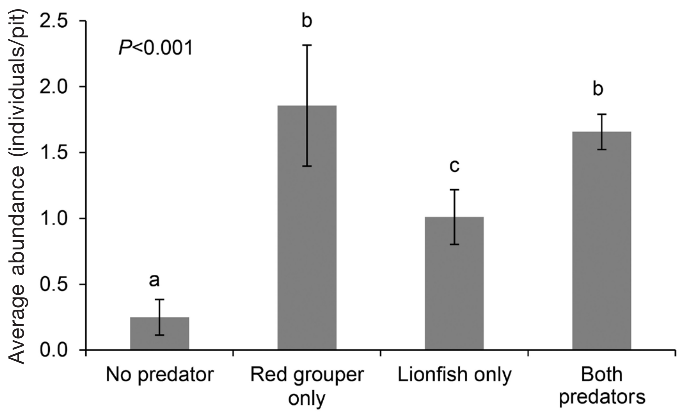

Figure 7

Average abundance, measured as number of individuals per grouper pit, of large fish, including large grunts such as the margate (*Haemulon album*) and cottonwick (*Haemulon melanurum*), snapper (*Lutjanus* spp.), grouper (*Mycteroperca* spp, *Epinephelus* spp., and the graysby, *Cephalopholis cruentata*), triggerfish (*Balistes* spp.), and the hogfish (*Lachnolaimus maximus*), associated with grouper pits surveyed during 2012–2015 off southwestern Florida, shown for each predator presence or absence category: no predator; red grouper (*Epinephelus morio*) only; species of lionfish (*Pterois* spp.) only; or both predators. The *P*-value is given for results from the Kruskal–Wallis test. Statistically significant differences are noted with different letters (a–c). Error bars indicate standard errors of the mean

was conducted by Albins (2013), native fish communities on shallow-water patch reefs in the Bahamas were compared when a native grouper (the coney [*Cephalopholis fulva*]), the lionfish, both predators together, and neither predator was present. Lionfish were found to cause a reduction in abundance of small, native coral-reef fishes 2.5 times greater than the reduction caused by the native piscivore. Lionfish also caused a reduction in the species richness of small coral-reef fishes, whereas the native piscivorous grouper had no significant effect. We observed no negative effects of presence of lionfish on the fish communities associated with mesophotic red grouper pits. Instead, pits with lionfish had both greater species diversity and species richness, and they had higher abundances of some fish species.

Although limited in number, other studies also have reported no negative effect from the invasion of lionfish. Elise et al. (2015), for example, found no significant change in the structure of the native fish assemblage or in species richness and density of potential lionfish prey, predators, and competitors over time with the arrival of lionfish in the Archipelago Los Roques National Park, Venezuela. In fact, species richness of predators and competitors of lionfish and density of predators of lionfish were higher where lionfish were present. They attributed this result to habitat characteristics and good abiotic conditions supporting high species richness and density of prey. Lionfish may therefore actively select areas where species richness and prey density are highest. Areas where lionfish are found may reflect not only favorable habitat for lionfish but also for native predators.

This explanation could also apply to Pulley Ridge. The effect of lionfish has not been documented previously for a habitat type such as grouper pits. These pits are essentially the only feature on the ridge with enough structural complexity to provide suitable habitat for both large predators and small reef fish. If high abundances of fish are actively recruiting to these pits, it is conceivable that an effect from lionfish would not be observed. An alternative explanation for the lack of a lionfish effect could be the length of time since lionfish have colonized the location. In the Albins (2013) study, during which a negative effect from lionfish was observed, data were collected 4 years after the presence of lionfish had been confirmed. In contrast, Elise et al. (2015) collected data just 1 year after lionfish were first sighted, and we began collecting data at Pulley Ridge just 2 years after lionfish were detected.

Red grouper, through their manipulation of the substrate of their habitat form structurally complex pits that play an important role in the dynamics of fish communities. Overexploitation of red grouper because of its economic value could have negative effects on biodiversity (Coleman and Williams, 2002), especially in an area like Pulley Ridge where the pits are one of the only features providing habitat refuge for any number of fish species. Although Pulley Ridge is protected, because of its status as an HAPC, the regulations (ban on longlines, trawling, and anchoring) primarily protect coral and sessile invertebrates and not any of the 12 economically valuable fish species. Conversely, hook-and-line fishing is still allowed in this otherwise protected area. The occurrence of hook-and-line fishing may explain why differences in abundance of red grouper were not observed inside versus outside the HAPC.

The presence of fish in grouper pits is significant for fisheries management because a change in pit activity and numbers may indicate the presence and abundance of economically important fish. Over time, a change in pit density may indicate changes in fish populations and could be used to either evaluate health of a stock or the effectiveness of a fishery closure. Wall et al. (2011), for example, recorded an increase in the number and density of pits from 2006 to 2009 in Steamboat Lumps MPA by mapping habitat with acoustic sonar. Gathering additional information on the variety and number of fish associated with the pits could be used to evaluate their populations as well (Scanlon et al., 2005). The data reported here on pits uninhabited and habited by red grouper will be useful for management and could be used to assess the long-term health and status of the important fish communities found in grouper pits.

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