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Characterization of the mesophotic reef fish community in south Florida, USA

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Summary

The southeastern coast of Florida, USA supports a substantial recreational fishery, yet little is known of the coral reef ecosystem or fisheries resources past 50 m depth. Fish assemblages associated with low-relief substrate and three vessel reefs between 50 and 120 m depth off southeast Florida were surveyed by remotely operated vehicles providing the first characterization of the mesophotic fish assemblages in the region. Two distinct assemblages were observed on low-relief substrate and high-relief vessel reefs. A total of 560 fishes of 42 species was recorded on 27 dives on low-relief substrate, and 50 152 fishes of 65 species were recorded on 24 dives on three vessel reefs. Small planktivorous Anthiinae fishes and several economically valuable species were common on vessel reefs but rare on low-relief substrate. Fish assemblages on vessel reefs more closely resembled those found at similar depths in high-relief natural areas off east-central Florida and the Gulf of Mexico than those associated with adjacent low-relief habitat or nearby coral reef tracts. From a fisheries perspective, these results provide limited support to the hypothesis that in deep-water regions with limited relief, vessel reefs may provide an opportunity to increase fish diversity and abundance by creating high-relief habitat without compromising adjacent fish assemblages.

Introduction

The southeastern United States continental shelf and shelf edge between 50 and 120 m depth supports a diverse and economically important reef-fish community (Miller and Richards, 1980; Grimes et al., 1982; Parker and Ross, 1986; Reed, 2002; Sedberry et al., 2006). Low-relief hardbottom, rocky outcrops, and deep-water coral reefs provide habitat for a variety of fish species. Despite the extent and importance of the mesophotic zone, the associated reef-fish assemblages are still poorly described in many regions due to difficulties inherent with working deeper than normal recommended SCUBA limits (40 m). As coral reef resources in the western Atlantic and Caribbean continue to decline (Gardner et al., 2003; Paddack et al., 2009), there is a renewed interest in possible deep-water refuge for species of concern (Kahng et al., 2010). This study provides the first characterization of reef fish associated with this depth zone in southeast Florida.

A few studies utilizing remotely operated vehicles (ROVs) and submersibles have described mesophotic reef-fish assemblages in the western Atlantic and Gulf of Mexico, i.e. northeastern and northwestern Gulf of Mexico, the South Atlantic Bight, and the Oculina Banks south of Cape Canaveral, Florida (Parker and Ross, 1986; Dennis and Bright, 1988; Gilmore and Jones, 1992; Weaver et al., 2001, 2006; Quattrini et al., 2004; Reed et al., 2005; Schobernd and Sedberry, 2009). Although these deep-reef areas differ in relief and invertebrate composition, the fish assemblages are generally similar. Deep reefs along the continental shelf have historically been important fishing grounds due to the occurrence of several lutjanid and serranid species. Reef-associated fauna such as pomacentrids, chaetodontids, pomacanthids and labrids are present, but typically deep-water congeners replace shallow-water species (Dennis and Bright, 1988). Herbivorous and omnivorous species were absent or rare in previous surveys and small planktivorous anthiine fishes numerically dominated the deep-reef fish assemblage (Weaver et al., 2001; Harter et al., 2009; Schobernd and Sedberry, 2009). These anthiine fishes are considered keystone species in the deep-reef food web (Weaver et al., 2001). Recent stock assessments suggest that nine species found in the deep-reef fish assemblage in the South Atlantic Management region are currently subjected to overfishing (National Marine Fisheries Service, 2011). The decline of these important species has led to an increased interest in the study of deep reefs and their associated fauna. Further, anthropogenic and environmental stressors negatively affect tropical coral reef-fish communities and the deep-water habitats may offer a refuge from these pressures.

The continental shelf offshore of southeast Florida, USA is unique compared to other regions surveyed as it is narrow, relatively steep, and consists of low-relief habitat (Malloy and Hurley, 1970; Avent et al., 1977; Mullins and Neumann, 1979). Other than a region of increased slope between 70 and 80 m depth, there are no known natural features with relief > 1 m between 50 and 120 m (Avent et al., 1977). The bottom habitat and fish assemblages at these depths off southeast Florida have not been studied. Although there are no major shelf-edge prominences known in the region, 22 artificial vessel reefs (sunken derelict ships) and numerous smaller structures have been placed at depths greater than 50 m to enhance recreational fishing. These structures offer high-relief habitat not naturally found in the region; yet, other than anecdotal fishing reports, little is known of the associated fish assemblages.

The fish assemblages on artificial structures in shallower water have received ample study (Bohnsack, 1989; Potts and Hubert, 1994; Rooker et al., 1997; Arena et al., 2007). These assemblages vary in similarity to natural assemblages and appear to be influenced by structural forms of habitat, time underwater, construction material, size, orientation, and depth. In southeast Florida, vessel reefs deployed at a depth of 20 m have different assemblage structures with greater

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species richness and abundance of fishes than surrounding natural substrate and appear to provide habitat for species colonization (Arena, 2005; Arena et al., 2007). However, there are few reports on fishes associated with artificial structures deeper than 50 m (Moffitt et al., 1989; Shinn and Wicklund, 1989; Stanley and Wilson, 1998) and other than reports from local fishers, technical divers, and one submersible study, little is known of fish assemblages associated with mesophotic vessel reefs (Shinn and Wicklund, 1989; Neugaard, 2003).

The goal of this study is to provide an initial characterization of the mesophotic reef-fish assemblage offshore south Florida. ROVs were used to survey low-relief habitat with multiple transects and extensively study three high-relief vessel reefs over time. Comparing fish assemblages associated with vessel reefs to neighboring low-relief habitat provides insight into diversity and abundance of species that associate with these habitats and this, in turn, should provide some insight into species-specific use and resource management potential of deep-water vessel reefs.

Methods

Two different ROVs were used for this project. The Benthic Observation Vehicle (BOV), built by Baxley Ocean Visions, Inc. was used during 2004 and the VideoRay Pro III XE GTO, manufactured by VideoRay LLC, was used from 2005 to 2007. Both ROVs were equipped with lights, depth sensor and a digital camera that recorded directly onto mini digital video tapes. It was our intention to use the same survey methods for both sites. However, ROV operational logistics, coupled with preliminary surveys, which showed a striking difference in fish abundance on low-relief habitat and vessel reefs, necessitated the use of two different survey methods to characterize the reef fish community.

Low-relief substrate

Timed transects were used to survey low-relief substrate since a greater area could be covered, which allowed for a more complete fish assemblage description. Twenty-seven transect start points were arbitrarily selected with consideration given to avoidance of known artificial structures (Figs 1 and 2). Survey depth ranged from 46 to 115 m and distance from 91 to 3074 m (Table 1). Survey direction, speed, and duration varied among transects and was dependent on prevailing winds, currents, and ROV performance. The ROV was attached to a 5–15 kg clump weight with 30 m of positively buoyant tether and 'flown' within 3 m of the bottom at approximately 0.5 m s^{-1}, depending on current. Transect length was determined by recording GPS coordinates and time when the ROV arrived and left the bottom. Fish were identified within visual range of the camera, approx. 3 m on either side of the transect line with minimal up-looking. Estimated visibility was typically 30 m but ranged from 20 to 35 m. Depth at which each fish was observed was recorded from video.

Vessel reefs

Three vessel reefs were surveyed. *Bill Boyd*, the largest vessel reef (65 m length), was located at 82 m depth in a region of increased slope. *Caicos Express* (56 m length) at 74 m depth was the shallowest vessel reef surveyed. *Papa's Reef* was the smallest vessel reef surveyed (52 m length) and laid at 80 m depth. All vessel reefs were freighters and were scuttled intact between 1985 and 1989.

A rotating schedule of one vessel reef survey per month was planned. However, various personnel, weather, and technical problems prohibited such, and ROV surveys were conducted opportunistically from March 2004 until July 2007. Strong currents and the complex vertical structure of vessel reefs, including multiple decks, cargo holds and superstructure, increased the risk of entangling the ROV and limited the effectiveness of transects. Therefore, a modified timed swim with a series of timed stationary counts was used.

The ROV was deployed from an anchored research vessel with 30 m of positively buoyant tether connected to 150 m of negatively buoyant, smaller diameter tether at a clump weight. Ideally, the clump weight was positioned directly adjacent to the vessel reef and, with 30 m of tether, the ROV was then 'flown' along the hull of the vessel reef in an attempt to view fish associated with all regions of the vessel. Stationary counts were also conducted along the vessel reef to aid in identification of small and semi-cryptic species. For the purpose of standardization, the reef-associated assemblage was defined by fishes within 3 m of the vessel reef, and only video taken within 3 m of vessel reefs was used for analyses.

Prior to 2 h before sunset, ambient light at depth was sufficient to conduct surveys. However, lights onboard the ROV were used when looking under the bow and stern, inside cargo holds, inside vessel reefs through scuttling holes, ports and doors and to aid in fish identification.

Analysis

Video from low-relief substrate and vessel reef surveys was viewed on a 70 cm screen monitor for fish identification. All fish were identified to the lowest identifiable taxon. Fish were classified as unidentified if family could not be determined and thus were not used for analysis. Location on the vessel reef, estimated size, diagnostic markings, and behavioral traits were used to reduce repeat counting of individual fish.

Fishes were categorized by trophic habit (benthic carnivore, general carnivore, herbivore, omnivore, planktivore, and piscivore) based on information obtained from FishBase (Froese and Pauly, 2011), and congeners were used when no information was available for a species. These categories are a panoptic summation of lifestyle attributes that may be confounded by a host of factors, such as seasonality, ontogeny or resource availability and are used here only as an aid in characterization.

In order to aide in the characterization of fish assemblages on the two different habitat types and to allow generalized comparisons to be made with other studies, relative abundance was measured as fish per video-h (hereafter, fish h^{-1}). Although abundance data were quantified with the same units (for both low-relief substrate and vessel reefs), the difference in methods used to collect data on low-relief substrate and vessel reefs confounded comparisons. In addition, each region of the vessel reefs did not receive equal survey time, mainly due to current conditions. Visibility and current also varied between surveys, both of which likely affected the number of species observed. These factors precluded statistical comparisons of differences between assemblages.

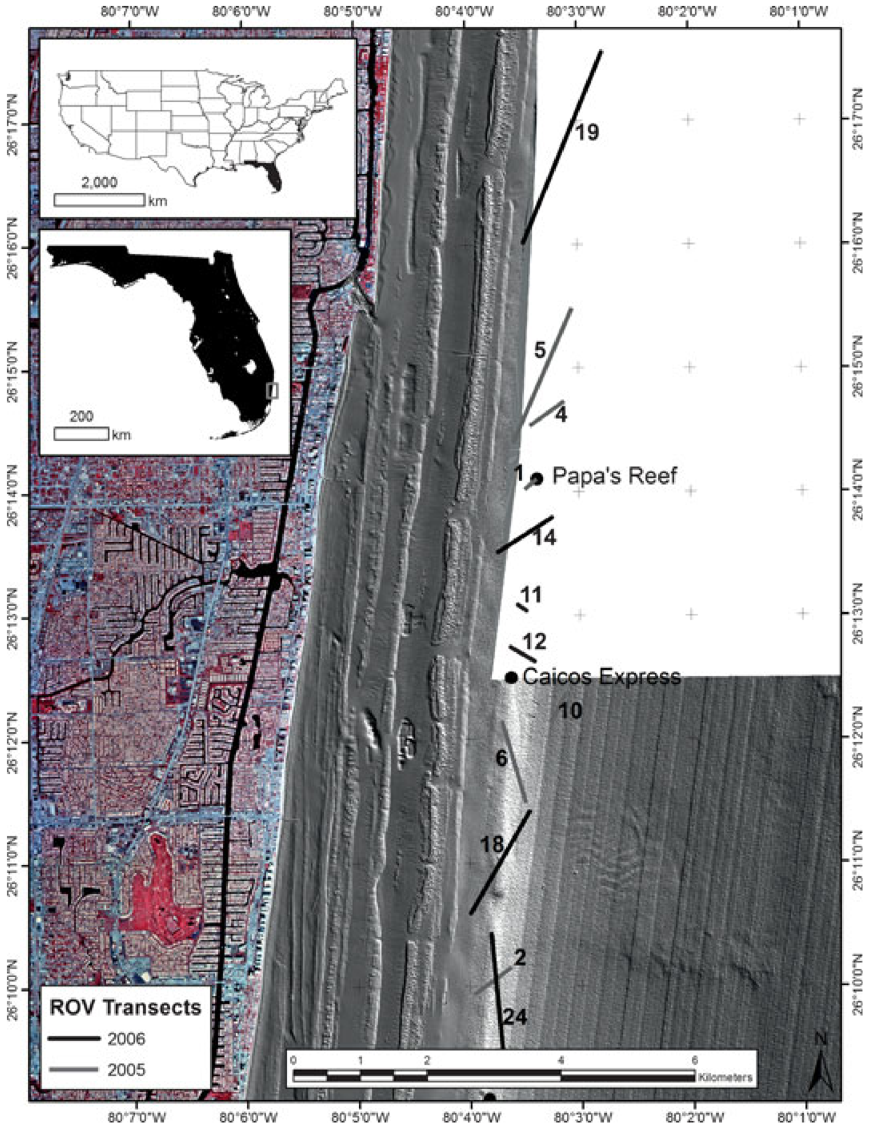

Fig. 1. Location of northern transects in reference to vessel reefs plotted on bathymetric hillshaded map. Bathymetric imagery for area not available in white

Results

Two distinct assemblages were observed on low-relief substrate and high-relief vessel reefs. A total of 50 712 fishes of 85 species was recorded on low-relief and vessel reefs combined. There were dramatically fewer total fish [33.8 fish h^{-1} (±12.1 SD) vs 2246.7 fish h^{-1} (±832.4 SD)] and fewer species (42 vs 65) counted on low-relief than on vessel reefs and only 20 species overlapped out of the 85 total (Table 2).

Low-relief substrate

Forty-two fish species were identified from 16.4 h of survey time during 27 transects along low-relief substrate (Table 2). Total counted on low-relief substrate was 560 fish, or 33.8 fish h^{-1}. The low-relief fish assemblage was composed of benthic carnivores, general carnivores, and a few planktivores. Only two piscivorous species (almaco jack, *Seriola rivoliana* and great barracuda, *Sphyraena barracuda*), one herbivore (*Acanthurus* spp.), and two omnivores (French angelfish, *Pomacanthus paru* and scrawled cowfish, *Acanthostracion quadricornis*) were recorded.

The low-relief substrate had little vertical relief > 0.3 m, and the majority of the region surveyed consisted of sand or small rubble that would provide limited refuge for most fishes. There appeared to be a change in substrate with depth. There were extensive regions of algae and rubble with antipatharian corals, octocorals, and occasional sponges < 0.3 m height between 50 and 60 m depth. Algae became sparse between 60 and 70 m depth and areas of sand and small rubble increased. Although there was more sand between 70 and 85 m depth, regions of increased slope consisted primarily of small rubble with occasional rocks larger than 0.5 m. Large sponges (0.3–0.6 m height), octocorals, and antipatharian corals were occasionally observed. Below 85 m depth the substrate was primarily sand. Despite a general lack of natural habitat with relief > 0.3 m, more than 100 small artificial structures were found, primarily solitary automobile tires and a few small tire groups. Generally, at least one fish, usually a serranid, was associated with each tire. Of fishes observed during low-relief substrate surveys, 21% were associated with these small structures.

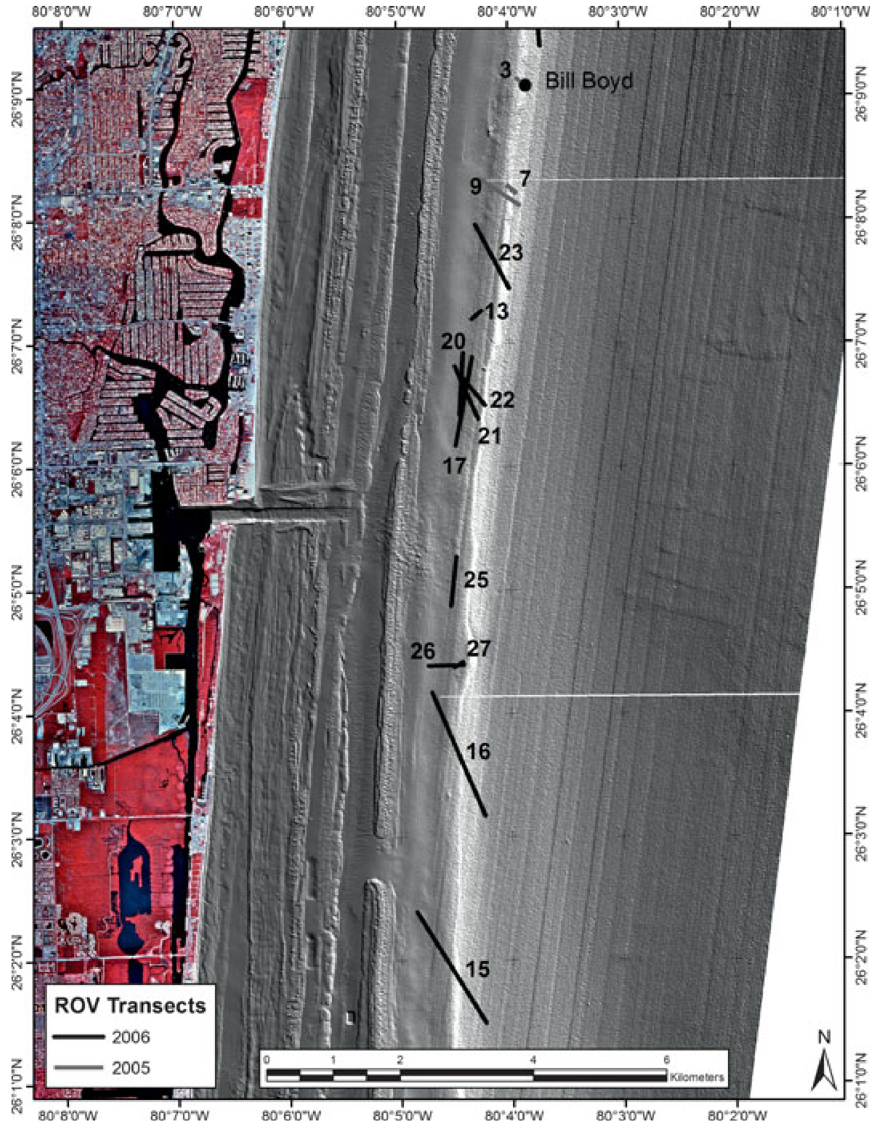

Fig. 2. Location of southern transects in relation to vessel reefs plotted on bathymetric hillshaded maps

Tattler bass, *Serranus phoebe*, were relatively common on low-relief habitat to a depth of 90 m. *S. phoebe* abundance was likely influenced by small artificial substrate, as 31% were found in association with tires. Bank sea bass, *Centropristis ocyurus,* were also commonly observed on low-relief substrate. At depths greater than 80 m, all *C. ocyurus* observed were associated with small artificial structures. Several short bigeye, *Pristigenys alta*, were observed between 60 to 90 m in association with higher relief rocks (0.3–0.6 m).

Blueline tilefish, *Caulolatilus microps*, and their associated burrows were recorded at a depth of 115 m. Although only two individuals were recorded, an abundance of burrows suggested a larger population. Four juvenile snowy grouper, *Hyporthodus niveatus*, were observed between 60 and 100 m depth, three of which were associated with small artificial structures. Likewise, 14 out of 18 hogfish, *Lachnolaimus maximus*, were observed in association with artificial structures.

Vessel reefs

Sixty-five fish species were recorded during 22.2 h of video from 24 vessel reef surveys (Table 2). *Bill Boyd* and *Caicos Express* were each surveyed nine times for a total of 8.5 and 7.1 h, respectively. *Papa's Reef* was surveyed six times for a total of 6.6 h. Total fish abundance on vessel reefs was dramatically greater (50 152 total; 2246.8 fish h^{-1}) than low-relief substrate.

A major difference in the fish assemblage between vessel reefs and low-relief substrate was anthiine fish abundance. Numerically, anthiine fish dominated vessel reefs (44 000+) while only 81 anthiine fish were recorded during low-relief substrate surveys. On average, [2000.0 fish h^{-1} (±966.2)] anthiine fish were observed on each vessel reef. Species identification of all anthiine fish was not possible. Several hundred roughtongue bass, *Pronotogrammus martinicensis,* were identified among the schools, but it appeared that at least one other anthiine species was present. Juvenile *H. niveatus* (10–20 cm total length [TL]) and juvenile speckled hind, *Epinephelus drummondhayi* (10–30 cm TL), were observed on vessel reefs. Fisheries important species such as amberjack, *Seriola dumerili*, *S. rivoliana*, scamp, *Mycteroperca phenax*, blackfin snapper, *Lutjanus buccanella*, gray snapper, *Lutjanus griseus* and vermillion snapper, *Rhomboplites aurorubens,* which were rare during low-relief surveys, were more common on vessel reefs.

Table 1
Drift transects over low-relief hardbottom

Drift no.	Survey date	Length (m)	Survey time (min)	Depth range (m)
1	March 05	244	31	50–76
2	March 05	685	56	60–95
3	April 05	91	57	64–70
4	May 05	631	52	58–95
5	May 05	2196	36	50–95
6	June 05	1274	26	73–76
7	June 05	207	30	64–98
8	June 05	NA	11	67–82
9	June 05	758	31	50–92
10	July 05	520	25	115
11	January 06	153	15	67–88
12	Janaury 06	416	26	67–85
13	April 06	188	15	55–60
14	May 06	959	117	50–113
15	July 06	1945	89	50–108
16	July 06	1845	63	50–104
17	July 06	1341	17	50–67
18	July 06	1754	43	46–100
19	July 06	3074	54	46–100
20	August 06	929	31	50–60
21	August 06	860	23	50–70
22	August 06	559	17	55–83
23	August 06	1084	22	55–105
24	August 06	1881	35	73–104
25	August 06	732	26	55–60
26	August 06	527	32	70–73
27	August 06	149	22	67–80
Total		25 002	1002	50–113

Discussion

The mesophotic zone offshore southeast Florida is characterized by two distinct fish assemblages. The first is a sparsely populated assemblage dominated by small solitary serranids, benthic carnivores, and transient general carnivores associated with a low-relief substrate that has little apparent refuge. The second is a more diverse assemblage of planktivores, benthic carnivores, and larger piscivores closely associated with high-relief vessel reefs with complex refuges of varying size. Both assemblages differ from assemblages found on natural substrate and vessel reefs in shallower water (Arena et al., 2007). However, the mesophotic reef-fish assemblages are similar to others observed at similar depths along the southeastern United States shelf and throughout the Gulf of Mexico (Weaver et al., 2001, 2006; Reed et al., 2005).

In an earlier version of this manuscript we pointed out, as we have here, that for technical reasons the data between the low-relief substrate and the vessel reefs was not amenable to rigorous statistical comparison. Nonetheless, we were criticized for the lack of statistical analysis and the reviewers offered suggestions how the data could be manipulated to allow such analysis. This is not a unique experience, but one worthy of discussion. Statisticians have repeatedly warned of the problems of relying heavily on statistical interpretation of biological data and have also pointed out that there are good studies not amenable to inferential statistical analysis (Hurlbert, 1984; Yoccoz, 1991). Yet many biologists, not particularly known as a group with great mathematical skill (an old joke about mathematicians has morphed into one about biologists: there are three kinds of biologists, those who can work with numbers and those who cannot), continue to ignore these caveats and routinely reject papers due to inadequate or inappropriate statistical analyses (Pautasso, 2010). Beyond question, most of these rejections are well deserved. However, in some cases this reliance on statistics appears to have led to the suspension of common sense. There is little reason to statistically verify an obvious difference (Deming, 1975). For example, in this study there was a ~70-fold difference in the characterizations of the low-relief and vessel reef fish abundances, a 35% difference in species richness, and <25% species similarity. It would add little to follow the previous statement with a P-value, and force fitting the data into some form to achieve it could be misleading. Further, the reliance on statistics has prevented good studies from being published because they failed to achieve the gold standard, $P < 0.05$, and, conversely, suspect data that was massaged statistically to be published (Rosenthal, 1979; Pautasso, 2010).

We are not 'casting stones' at reviewers who are, after all, operating within the accepted paradigm of the discipline and, obviously, statistical analysis is a critical tool in data interpretation and we are not suggesting otherwise. However, we question whether the current reliance on statistics is a bit excessive in Biology and if it is time to take a more holistic approach.

Low-relief habitat

Species richness (42) along low-relief habitat in the mesophotic zone between 50 and 120 m depth is low and comparable to submersible surveys at similar depth along the continental shelf in the South Atlantic Bight and Gulf of Mexico (Parker and Ross, 1986; Dennis and Bright, 1988; Lindquist and Clavijo, 1993). However, unlike these areas, the 50 m depth contour in southeast Florida is directly adjacent (<1 km) to a diverse coral reef tract that harbors 173 species (Ferro et al., 2005). With this in mind, it is interesting to find such a depauperate fish community, especially at the 50–60 m depth where algae, sponges, and octocorals thrive. Pomacanthid, scarid, and acanthurid fishes, abundant at depths <30 m throughout the Caribbean and Gulf of Mexico, were almost completely absent (Humann and DeLoach, 2002). The serranids, lutjanids, and haemulids were also rare. Low diversity may be an indicator of poor habitat availability, as many species found on the adjacent shallower water reef tract have greater depth ranges and can be found further north in more rugose habitat and relatively cooler waters (Miller and Richards, 1980; Parker and Ross, 1986; Ferro et al., 2005; Brokovich et al., 2008). Furthermore, Garcia-Sais (2010) observed a change and loss of diversity and abundance with depth and contributed this to reduced habitat complexity.

Although there was a general lack of suitable refuge throughout the 50–120 m depth zone, numerous artificial structures <1.0 m^2 were present. Some were unidentifiable objects, but the majority was automobile tires that offered a unique habitat for the region and had a fish assemblage similar to that observed elsewhere on small patchy habitat along the continental shelf (Parker and Ross, 1986). A few economically important species were observed on low-relief substrate. Of these, *H. niveatus* has recently received attention because the South Atlantic stock has been declared overfished, and stock rebuilding actions have been implemented (NMFS, 2011). Juvenile *H. niveatus* have been observed in shallower water (<50 m) and are associated with artificial structures in the Florida Keys and in southeast Florida at depths as shallow as 12 m depth (Moore and Labisky, 1984;

Table 2
Number of individuals recorded per hour for vessel reefs and low-relief substrate (numbers in brackets include those found on small artificial structures). Diet categorized as benthic carnivore (BC), general carnivore (GC), herbivore (H), omnivore (O), planktivore (PL), and piscivore (PI). Total survey time for vessel reefs and depth categories presented below each heading

			Vessel reefs			Low-relief substrate		
Common name	Scientific name	Diet	Bill Boyd 8.5 h	Caicos Express 7.1 h	Papa's Reef 6.6 h	50–70 m 7.8 h	71–90 m 5.4 h	91–120 m 3.2 h
Eagle Rays	Myliobatidae							
Spotted eagle ray	*Aetobatus narinari*	GC					0.19	
Morays	Muraenidae							
Morray spp.	*Gymnothorax* spp.	GC				0.13		
Batfish	Ogcocephalidae							
Longnose batfish	*Ogcocephalus corniger*	GC				0.26		
Squirrelfish	Holocentridae							
Squirrelfish	*Holocentrus adscensionis*	BC	0.24	2.52		0.13		
Cardinal soldierfish	*Plectrypops retrospinis*	BC		0.42	0.30			
Cornetfish	Fistularidae							
Bluespotteds cornetfish	*Fistularia tabacaria*	GC				0.26		
Sea Basses	Serranidae							
Graysby	*Cephalopholis cruentata*	PI		0.14				
Speckled hind	*Epinephelus drummondhayi*	GC	1.41	0.28				
Goliath grouper	*Epinephelus itajara*	GC		0.14				
Warsaw grouper	*Epinephelus nigritus*	GC		0.14	0.30			
Snowy grouper	*Epinephelus niveatus*	GC		0.14	0.91	0.13	[0.37]	[0.31]
Black grouper	*Mycteroperca bonaci*	PI	0.47	0.28	0.15			
Gag grouper	*Mycteroperca microlepis*	GC	0.24	0.14				
Yellowmouth grouper	*Mycteroperca interstitialis*	PI		0.14				
Scamp	*Mycteroperca phenax*	PI	5.76	7.01	3.48			
Creole-fish	*Paranthias furcifer*	PL		5.19				
Wrasse bass	*Liopropoma eukrines*	GC	0.59	1.12	1.06			
Spanish flag	*Gonioplectrus hispanus*		0.35	0.84	0.30			
Bank seabass	*Centropristis ocyurus*	GC					[0.37]	[4.66]
Tattler bass	*Serranus phoebe*	BC				1.15 [0.13]	4.07 [2.41]	
Roughtongue bass	*Pronotogrammus martinicensis*	PL	29.53	22.71	39.70		2.96	
Anthiine fishes	Anthiinae	PL	2519.41	857.52	2526.82		2.78	[15.54]
Greater soapfish	*Rypticus saponaceus*	GC	0.47	2.10	0.76			
Bigeyes	Priacanthidae							
Bigeye	*Priacanthus arenatus*	GC					0.19	
Short bigeye	*Pristigenys alta*	GC				0.51 [0.13]	3.89	
Cardinalfish	Apogonidae							
Bigtooth cardinalfish	*Apogon affinis*	PL			0.61			
Twospot cardinalfish	*Apogon pseudomaculatus*	PL			0.30	0.13		
Tilefish	Malacanthidae							
Blueline tilefish	*Caulolatilus microps*	GC						0.62
Sand tilefish	*Malacanthus plumieri*	GC				0.38		
Cobias	Rachycentridae							
Cobia	*Rachycentron canadum*	GC	0.47				2.41	
Remoras	Echeneididae							
Sharksucker	*Echeneis naucrates*	GC			0.15			
Jacks	Carangidae							
Bar jack	*Carangoides ruber*	GC	1.06	2.52	4.70	0.13		
Blue runner	*Caranx crysos*	GC		0.14		0.90		
Amberjack	*Seriola dumerili*	GC	8.47	3.64	2.73	0.77	9.81	1.24
Almaco jack	*Seriola rivoliana*	PI	14.47	3.50	4.24	0.51 [0.51]	1.48	
Permit	*Trachinotus falcatus*	BC			0.15			
Snappers	Lutjanidae							
Black snapper	*Apsilus dentatus*	GC		0.14				
Mutton snapper	*Lutjanus analis*	GC	0.12	0.42	0.15			
Blackfin snapper	*Lutjanus buccanella*	GC	1.65	9.53	5.30			
Lane snapper	*Lutjanus synagris*	GC		9.39				
Gray snapper	*Lutjanus griseus*	GC	28.59	21.17	8.94			
Cubera snapper	*Lutjanus cyanopterus*	GC	0.24	0.42				
Mahogony snapper	*Lutjanus mahogoni*	GC				0.13		
Vermilion snapper	*Rhomboplites aurorubens*	GC	95.88		36.52		8.52	3.42
Grunts	Haemulidae							
Black margate	*Anisotremus surinamensis*	GC	0.82	2.24	1.97			
Porkfish	*Anisotremus virginicus*	BC	2.94	0.70	0.30			

Table 2
(continued)

Common name	Scientific name	Diet	Vessel reefs: Bill Boyd 8.5 h	Vessel reefs: Caicos Express 7.1 h	Vessel reefs: Papa's Reef 6.6 h	Low-relief substrate: 50–70 m 7.8 h	Low-relief substrate: 71–90 m 5.4 h	Low-relief substrate: 91–120 m 3.2 h
Tomtate	*Haemulon aurolineatum*	GC	30.47	259.35				
Sailors choice	*Haemulon parra*	GC			0.15			
White grunt	*Haemulon plumieri*	GC		0.14				
Porgies	Sparidae							
Jolthead porgy	*Calamus bajonado*	BC	0.12		0.30			
Sheepshead porgy	*Calamus penna*	BC				0.64		
Drums	Sciaenidae							
Cubbyu	*Paraques umbrosus*	BC	1.65	3.64	9.24			
Blackbar drum	*Paraques itawamoto*	BC		0.42	1.67			
Spadefishes	Ephippidae							
Spadefish	*Chaetodipterus faber*		2.00		0.61			
Butterflyfish	Chaetodontidae							
Bank butterflyfish	*Prognathodes aya*	BC	6.71	6.03	5.76		0.56	[0.31]
French butterflyfish	*Prognathodes guyanensis*	O	0.12		1.06			
Reef butterflyfish	*Chaetodon sedentarius*	BC	1.88	7.29	1.97	0.38 [0.51]	0.37	
Angelfish	Pomacanthidae							
Blue angelfish	*Holacanthus bermudensis*	BC	0.35	0.56				
Queen angelfish	*Holacanthus ciliaris*	BC	0.35		0.15			
Rock beauty	*Holacanthus tricolor*	O		0.14				
Gray angelfish	*Pomacanthus arcuatus*	O	0.24					
French angelfish	*Pomacanthus paru*	O	0.47	0.28		0.64		
Damselfish	Pomacentridae							
Blue Chromis	*Chromis cyanea*	PL			0.15			
Yellowtail reeffish	*Chromis enchrysurus*	PL	2.71	6.03	0.91	2.05	0.19 [0.19]	
Purple reeffish	*Chromis scotti*	PL		0.14				
Sunshinefish	*Chromis insolata*	PL		4.77				
Damselfish	*Stegastes* sp.	O		0.56				
Wrasses	Labridae							
Spotfin hogfish	*Bodianus pulchellus*	BC	7.76	9.53	3.79	[0.13]		
Hogfish	*Lachnolaimus maximus*	BC	0.82	1.40	0.76	0.26 [1.67]	0.37	[0.31]
Wrasse species	*Halichoeres* sp.	BC	1.29	0.84	2.73	0.26	0.37	
Razorfish species	*Hemipteronotus* sp.	GC				0.13		
Parrotfishes	Scaridae							
Parrotfish	*Sparisoma* sp.	H		0.14				
Barracuda	Sphyraenidae							
Great barracuda	*Sphyraena barracuda*	PI	0.12	0.42	0.15		0.19	
Hovering Gobies	Ptereleotridae							
Blue goby	*Ptereleotris calliura*	PL	0.24			0.26	0.37	
Hovering gobies	*Ptereloetris* spp.	PL				2.05	3.15	
Surgeonfish	Acanthuridae							
Surgeonfish species	*Acanthurus* spp.	H				0.26		
Flying Gurnards	Dactylopteridae							
Flying gurnard	*Dactylopterus volitans*	GC				0.13		
Lefteye Flounders	Bothidae							
Flounder species	*Bothidae* sp.					0.13	0.19	
Scorpionfish	Scorpaenidae							
Spotted scorpionfish	*Scorpaena plumieri*	GC		0.14	0.45			
Filefish	Monacanthidae							
Unicorn filefish	*Aluterus monoceros*	BC			0.91	1.28		
Boxfish	Ostraciidae							
Scrawled cowfish	*Acanthostracion quadricornis*	O				0.51		
Trunkfish species	*Lactophyrs* spp.	BC				0.38		
Leatherjackets	Balistidae							
Gray triggerfish	*Baliste capriscus*	BC				8.33 [0.38]	2.04	
Puffers	Tetraodontidae							
Bandtail puffer	*Sphoeroides splengeri*	BC				0.51	0.19	
Goldface toby	*Canthigaster jamestyleri*	BC	0.24	1.40	0.15			
Puffer species	*Sphoeroides* sp.	BC	0.12					
Spiny Puffers	Diodontidae							
Burrfish species	*Chilomycterus* spp.	BC				0.13	0.19	

Arena et al., 2004). The juveniles observed on tires in this study were two to three times larger (10–20 cm TL) than juveniles found in shallower water (Arena et al., 2004). Although juveniles were also observed on vessel reefs, no adult *H. niveatus* were recorded in this study. However, in southeast Florida, adult *H. niveatus* are commercially caught between 120 and 260 m depth and are known to associate with deeper vessel reefs in other regions (Moore and Labisky, 1984; Bielsa and Labisky, 1987; Quattrini and Ross, 2006). They appear to be found only in association with or within close foraging distance of bottom structures and have a trend of increasing size with depth (Dodrill et al., 1993; Wyanski et al., 2000). It is possible that tires, vessel reefs, and other artificial debris in southeast Florida serve as transitional habitat for *H. niveatus* as they migrate from nearshore artificial structures to deeper waters as adults.

Vessel reefs

Whereas the low-relief artificial structures in southeast Florida offer habitat for small solitary species, vessel reefs provide highly complex vertical relief for a variety of species (65). Planktivores, general carnivores, benthic carnivores, and piscivores numerically dominated deep vessel reefs. Only five omnivorous species (21 total fish) and one herbivorous fish (a single *Sparisoma* sp.) were recorded. Haemulidae, a speciose and common reef fish family in the greater Caribbean area including Florida (Jordan et al., 2004), was relatively poorly represented on mesophotic zone vessel reefs. Vessel reef assemblages differ from those found in adjacent shallower waters and more closely resemble fish assemblages found on other high-relief structures at a similar depth in other regions.

A defining characteristic of shelf-edge reefs is the presence of large numbers of anthiine fishes (Lindquist and Clavijo, 1993; Koenig et al., 2000; Weaver et al., 2001; Quattrini and Ross, 2006). These planktivores have been considered a keystone predator for their role in the trophic food web and are a major difference between deep- and shallow-water fish assemblages in the western Atlantic and Gulf of Mexico (Weaver et al., 2001). These smaller planktivores appear to prefer higher relief structures and the associated vertical and elliptical eddies (Lindquist and Pietrafesa, 1989; Arena et al., 2007). Their abundance on vessel reefs provides an important link in the food web and is likely responsible for the greater number of piscivores and general carnivores. Direct observation in this study of a school of *S. rivoliana* feeding on anthiine fishes, provided additional support for this hypothesis.

In addition to high anthiine abundances, vessel reefs were also similar to other shelf-edge reefs with the occurrence of large carangids, serranids, and lutjanids. *S. dumerili* and *S. rivoliana* that are not common in shallow waters in southeast Florida, but were the most common large predators on deep vessel reefs (Ferro et al., 2005; Arena et al., 2007) (Table 1). Although it is difficult to make comparisons with other regions, the abundance of large serranids on vessel reefs appeared to be low. Quantitative data for abundances of fishes, particularly deep-reef fishes in the absence of, or with low fishing pressure are rare. Early studies on the Oculina Banks before they were damaged by trawls suggest that high relief substrate can support high seasonal densities of serranids (Gilmore and Jones, 1992). *Mycteroperca phenax,* an economically important species, was the most common serranid on vessel reefs (five per survey) yet rarely was an individual >50 cm TL (minimum fisheries size limit) observed (Harris et al., 2002). The lack of large *M. phenax* on vessel reefs may be another indication of fishing pressure in southeast Florida (Ferro et al., 2005).

Several economically important lutjanids were observed on vessel reefs. Juvenile *L. buccanella* have been recorded on shallower (20 m depth) vessel reefs (Arena et al., 2004) and other artificial habitat in waters <10 m depth (personal observation). Adults are typically found along the rocky ledges of the continental shelf at depths between 60 and 91 m (Robins and Ray, 1986). Adult *L. buccanella* were common on vessel reefs, yet were not observed on the natural substrate. It is possible that deep vessel reefs are providing habitat for *L. buccanella* during, or after, their ontogenetic offshore migration.

In addition to similarities in anthiine fish abundance and economically important species, vessel reefs have several other species in common with other high-relief shelf-edge habitats. Spotfin hogfish, *Bodianus pulchellus*, was one of the ten most abundant fish observed and appear to have completely replaced their shallower water congener, Spanish hogfish, *Bodianus rufus*. Vessel reefs also appeared to offer habitat for two sciaenids, the blackbar drum, *Pareques iwamotoi,* which has not been previously reported in southeast Florida, and cubbyu, *Paraques umbrosus*, which is uncommon-to-rare in shallower waters. French butterflyfish, *Prognathodes guyanensis*, an insular eurythermic species typically found in deeper waters (60–230 m) throughout the Caribbean, was recorded on *Papa's Reef* and once on *Bill Boyd. Prognathodes guyanensis* has only recently been described in continental United States waters (Quattrini et al., 2004), and this is the first record of the fish in southeast Florida.

In summary, this study provides the first detailed reef fish characterization of a relatively unexplored ecosystem susceptible to change (Lesser and Slattery, 2011). Only a small portion of the southeast Florida mesophotic zone was surveyed but the information provided establishes a baseline from which to initiate future research and management projects.

The natural habitat in southeast Florida between 50 and 120 m depth consists of low-relief substrate sparsely inhabited by a few solitary benthic carnivores, several transient piscivores, and general carnivores. Diversity and abundances of fishes are substantially lower than reported on adjacent shallower reefs. Although several species are found on adjacent shallow reefs, the fish assemblage between 50 and 120 m depth more closely resembles assemblages found in other regions at similar depth along the continental shelf. Numerous species observed during low-relief substrate surveys were associated with various small artificial structures. These structures appear to be providing habitat in a region where habitat is limiting and may be beneficial for some economically important fishes, such as *H. niveatus*.

In sharp contrast to low-relief substrate, the fish assemblage associated with high-relief vessel reefs is relatively abundant and consists of small planktivores, various general and benthic carnivores, and several large piscivores. A striking feature of the fish assemblages associated with vessel reefs is the presence of thousands of anthiine fishes that are an integral component of deep reefs as they transfer energy from the water column to the reefs. Their presence on vessel reefs is probably responsible for the occurrence of several economically important species including adult *S. rivoliana*, *S. dumerili*, *M. phenax*, *L. griseus,* and juvenile *H. niveatus* and *E. drummondhayi,* which are not common on low-relief substrate.

This study only examined relatively small portions of the natural substrate between 50 and 120 m depth. Furthermore, there are unquestionably species-specific and ontogenetic differences in movement onto vessel reefs not examined here. Nonetheless, based on the differences in species utilization of the differing habitats, it appears in general that the vessel reefs are not compromising fish assemblages on neighboring substrate or shallow reefs. The vessel reefs provide additional habitat in a region where habitat is limiting and increase the diversity of the deep fish community in southeast Florida. Economically important species are present on vessel reefs but observed sizes and abundances suggest current fishing pressure may not be at the same intensity as in shallower water. However, more research is required before vessel reefs can be recommended as a fisheries management tool. Fishing activity is high in southeast Florida, and although vessel reefs appear to be highly productive sites it is unlikely they can maintain, much less provide, surplus production of fisheries targeted species.

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