Abstract—A portion of the Oculina Bank located off eastern Florida is a marine protected area (MPA) preserved for its dense populations of the ivory tree coral (*Oculina varicosa*), which provides important habitat for fish. Surveys of fish assemblages and benthic habitat were conducted inside and outside the MPA in 2003 and 2005 by using remotely operated vehicle video transects and digital still imagery. Fish species composition, biodiversity, and grouper densities were used to determine whether *O. varicosa* forms an essential habitat compared to other structure-forming habitats and to examine the effectiveness of the MPA. Multivariate analyses indicated no differences in fish assemblages or biodiversity among hardbottom habitat types and grouper densities were highest among the most complex habitats; however the higher densities were not exclusive to coral habitat. Therefore, we conclude that *O. varicosa* was functionally equivalent to other hardbottom habitats. Even though fish assemblages were not different among management areas, biodiversity and grouper densities were higher inside the MPA compared to outside. The percentage of intact coral was also higher inside the MPA. These results provide initial evidence demonstrating effectiveness of the MPA for restoring reef fish and their habitat. This is the first study to compare reef fish populations on *O. varicosa* with other structure-forming reef habitats and also the first to examine the effectiveness of the MPA for restoring fish populations and live reef cover.

Assessment of fish populations and habitat on Oculina Bank, a deep-sea coral marine protected area off eastern Florida

Stacey L. Harter (contact author)[1]

Marta M. Ribera[1]

Andrew N. Shepard[2]

John K. Reed[3]

Email address for contact author: stacey.harter@noaa.gov

[1] National Marine Fisheries Service
Southeast Fisheries Science Center
3500 Delwood Beach Rd.
Panama City, Florida 32408

[2] NOAA Undersea Research Center
University of North Carolina at Wilmington
5600 Marvin Moss Lane
Wilmington, North Carolina 28409

[3] Harbor Branch Oceanographic Institute
Florida Atlantic University
5600 U.S. 1 North
Ft. Pierce, Florida 34946

Like shallow tropical coral reefs, deep-sea coral habitats support important ecosystem functions, for example, as hotspots for biodiversity and biomass production (Husebo et al., 2002; Jonsson et al., 2004; George et al., 2007) and as important fish habitat (Gilmore and Jones, 1992; Fosså et al., 2002; Ross and Quattrini, 2007). Like their shallow-water counterparts, deep-sea coral ecosystems are affected by human activities. As harvests have declined in shallow ecosystems, fishing pressure has moved further offshore (Watling and Norse, 1998; Koslow et al., 2000; Roberts, 2002), thus raising interest in deep-sea coral ecosystem protection. With the passage of the Magnuson-Stevens Fishery Management and Conservation Act of 1996, an ecosystem approach to fishery management in the United States has been encouraged by linking the preservation of essential fish habitat with protection of fishery resources. Reauthorization of the Act in 2006 mandated the conservation and studies of deep-sea coral ecosystems. These mandates are expected to lead to the increasing use of marine protected areas (MPAs) as a fishery management tool (Allison et

al., 1998; Bohnsack, 1998; Guenette et al., 1998).

One of the world's first deep-sea coral ecosystems to be designated a marine protected area is located approximately 37 km off Florida's east coast in depths of 60–120 m. This area is known as the Oculina Bank, a series of reefs and high-relief bioherms (thickets of live coral, capping mounds of sediment and coral rubble, built upon an underlying lithified base structure) constructed by the scleractinian ivory tree coral (*Oculina varicosa*). This species lives in water depths of 49 to 152 m without zooxanthellae and may form extensive thickets 1 m tall, which over thousands of years have built up mounds and ridges extending as much as 200 m laterally and 35 m above the surrounding seafloor (Reed, 1980). These *O. varicosa* bioherms are known to exist only off the east coast of Florida from Ft. Pierce to St. Augustine, a stretch of almost 150 km along the edge of the Florida-Hatteras slope and beneath the western edge of the Gulf Stream. Surface water currents may exceed 150 cm/sec and bottom currents may exceed 50 cm/sec (Reed, 2002a). Intact, live *O. varicosa* sup-

ports a diverse and dense assemblage of invertebrates and fishes (Avent et al., 1977; Reed, 2002a, 2002b; Koenig et al., 2005), and it may serve as spawning grounds for a number of economically important or threatened reef fish species (Gilmore and Jones, 1992; Koenig et al., 2005).

A portion of the Oculina Bank known as the Oculina Habitat Area of Particular Concern (OHAPC) first received protection in 1984 (Koenig et al., 2005; Reed et al., 2005). Current management regulations established by the South Atlantic Fishery Management Council include a 1029 km² (300 nm²) OHAPC (Fig. 1), within which bottom-fishing gear such as trawls, dredges, longlines, traps, and anchors are not permitted, in order

to protect the fragile coral. Within the OHAPC, the 315 km² (92 nm²) Oculina Experimental Closed Area (OECA) (Fig. 1) was designated in 1994 in response to the rapidly diminishing grouper (*Mycteroperca* and *Epinephelus* spp.) populations and excludes all bottom fishing, including fishing with hook-and-line gear, in order to assess the use of a MPA for recovering over-fished reef fish populations, especially those of grouper.

Management requirements to protect many deep-sea coral ecosystems have been delayed owing to the difficulty in quantifying, monitoring, and restoring damaged reefs (Pyle, 2000). Despite efforts to understand and protect the Oculina Bank, extensive damage to the fragile coral had already occurred from fishing gear prior to the implementation of management regulations (Koenig et al., 2000; Reed et al., 2007). When the first management action was taken in 1984, only about 30% of the reef system was afforded protection (Reed et al., 2005). Fishing, including shrimp trawling, was allowed to continue in the northern section of the Oculina Bank until the OHAPC was expanded in 2000. Decades of shrimp trawling and scallop dredging before protection had reduced most of the 150-km stretch of healthy reefs to coral rubble (Reed et al., 2007). Remotely operated vehicle (ROV) transects and multi-beam mapping surveys since 2000, however, have indicated that Jeff's Reef and Chapman's Reef, both located in the southern portion of the OECA, still contain a large amount of intact live *O. varicosa* (Fig. 1) (Reed et al., 2005).

Over-fishing has significantly diminished populations of reef fishes, especially those of groupers (Koenig et al., 2000, 2005). Historical observations made during the 1970s and 1980s indicate that *O. varicosa* reefs were once dominated by large groupers, but later surveys found grouper populations greatly diminished and the reefs dominated by small, non-fishery species like small sea basses (*Serranus* and *Centropristis* spp.), butterflyfishes (*Chaetodon* spp.), and damselfishes (*Chromis* spp.) (Koenig et al., 2005).

A current topic of discussion regarding deep water corals is whether they serve as essential habitat for some fish species or whether any type of 3-dimensional structure (e.g., rock ledges) is important. Auster (2005) proposed that examination of the distribution of fish in relation to all available habitats is one method to assess the "essential"
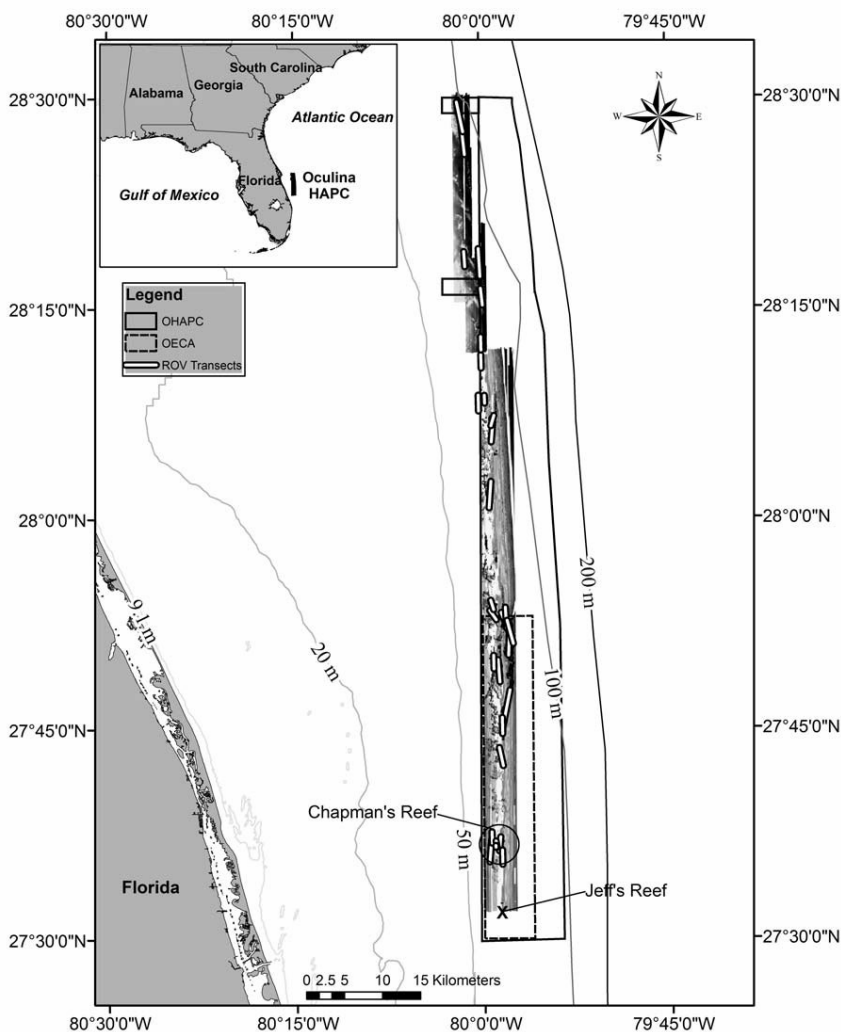

Figure 1

Remotely operated vehicle (ROV) transects overlain on the multi-beam map of the Oculina marine protected area (MPA) off eastern Florida. Location of the OHAPC and OECA (OHAPC=areas where all bottom gear except hook and line are restricted, i.e., excluding the OECA, and OECA=inside the MPA where all bottom gear, including hook and line fishing, are restricted) are shown along with Chapman's and Jeff's Reefs. ROV transects were conducted during April–May 2003 and October 2005.

role of deep water corals. Several studies have concluded that deep water corals were no more important to fishes than other reef structures (Auster, 2005; Tissot et al., 2006) suggesting an opportunistic fish association with deep corals. Ross and Quattrini (2007), however, found that deep reef habitats along the southeast United States slope contain a unique and possibly obligate assemblage of fish. No previous studies have examined whether *O. varicosa* supports a distinct assemblage of fish compared to other structure-forming, hardbottom habitats.

In 2014, the South Atlantic Fishery Management Council will re-evaluate the effectiveness of the OECA. To aid the Council in making future management decisions, our goals for this project were to (1) compare fish assemblage composition, biodiversity, and grouper densities among hardbottom reef habitat types to examine whether *O. varicosa* is an essential habitat structure compared to other structure-forming reef habitats; (2) compare fish assemblage composition, biodiversity, and grouper densities inside and outside managed areas to assess the effectiveness of the MPA; and (3) quantify the percent cover of all hardbottom habitat types.

Materials and methods

Sampling design

In 2002 and 2005, multibeam maps (3-m resolution) were produced for a portion of the Oculina Bank. Coverage included 90% of *O. varicosa* bioherms thought to occur inside the OHAPC, and a portion of bioherms outside the OHAPC between the two satellite areas (Fig. 1). These maps were used to select remotely operated vehicle (ROV) transect stations (April–May 2003, October 2005) so that all habitat types and management areas were examined. Management areas sampled included open (any area outside the OHAPC open to fishing), OHAPC (areas where all bottom gear except hook and line are restricted, i.e., excluding the OECA), and OECA (inside the MPA where all bottom gear, including hook and line fishing, are restricted).

Locations of ROV dive transects were non-random and were based on conducting an equal number of dives in each management area. Due to high current speeds, all dives were conducted in a northerly direction (drifting with prevailing Gulf Stream current with minimal east-west maneuvering). The starting points were chosen *a priori* in order to have each dive cover a range of the major substrate types (described below) as indicated from the multibeam maps. Dives ranged from 0.5 to 3.5 hours.

In addition to management area, fish assemblages were analyzed among five major hardbottom habitat types. Habitat types used were a subset of the Southeast Area Monitoring and Assessment Program (SEAMAP) habitat classification scheme and included pavement, rubble, rock outcrops, standing dead *O. varicosa* coral, and live *O. varicosa* coral. One difference between our habitat classification and that of SEAMAP is that we distinguished between live and dead coral. Pavement habitat was fairly flat rock pavement often with small cracks or crevices present. Rubble habitat consisted of small coral fragments exhibiting little to no relief. Rock outcrop habitat was small rock outcrops approximately 0.3–0.9 m relief, occasionally 1.2–1.8 m relief. *O. varicosa* existed mostly as small individual heads (about 0.3–0.9 m relief), but occasionally as larger mounds and thickets.

Collection methods

The *Phantom Spectrum II* ROV (National Undersea Research Center, University of North Carolina at Wilmington) was used to conduct video and digital still transects to estimate fish densities and characterize habitat. A downweight (~145 kg) was tethered to the umbilical cable of the ROV and the ROV was tethered to a 30-m leash, which allowed it to run just above the seafloor (<1 m) at a controlled over-the-ground speed of approximately 0.39 m/s (range 0.26 to 0.77 m/s). The geographic position of the ROV was constantly recorded throughout each dive using a slant range positioning system linked to the ship's Global Positioning System (GPS). The ROV was equipped with lights, lasers, forward-looking video camera, and down-looking still camera. Lasers projected parallel beams 10 cm apart for measuring fish and habitat features. The forward-looking color video camera provided continuous video while the down-looking high-resolution digital still camera captured images of fish and habitat.

Fish population analyses

Fishes were identified to the lowest discernable taxonomic level and counted and the habitat types were classified from video covering 50-m (±2.5 m) transects. Excluded from the analysis were sections of video recorded when the ROV was in non-hardbottom habitats, video clouded by stirred up sediment, video that zoomed in on a species of interest, or video recorded when the camera was elevated in the water column.

Fish densities (numbers/hectare) were determined by estimating the area viewed during video transects from transect length (*L*) and width (*W*). Transect length was calculated from latitude and longitude recorded by the ROV tracking system. Width of each transect was calculated using the following equation:

$$W = 2(\tan(^1/_2 A))D, \qquad (1)$$

where *A* = horizontal angle of view (a constant property of the video camera); and

D = distance from the camera at which fishes could be identified with certainty.

D was usually 5 m except for some dives in 2005 where visibility was reduced to 2–3 m. In 2003, a set of three lasers was mounted to the ROV. The lasers were set up

so that when they were projecting out at a distance of 5 m, two of the lasers overlapped. The third laser was spaced 10 cm apart from the two overlapping lasers, which allowed measurements to be made. This was initially used to train the eye to determine the distance at which fishes could be identified. Distance was then estimated on subsequent dives in 2005. Transect area (*TA*) was then calculated as:

$$TA = (LW) - \tfrac{1}{2}(WD) \quad \text{(Koenig et al., 2005).} \quad (2)$$

Mean *TA* was 372.9 m² ±1.8 m². Density of all observed fish species was calculated for each transect in 2003 and 2005. Initial analyses demonstrated that no statistical differences were evident between years, so data from both years were combined for all analyses.

Multivariate ecological analyses were conducted using PRIMER 5.0 (Primer–E Ltd, Plymouth, U.K.) to examine fish assemblage composition among habitat types and management areas. A non-metric multi-dimensional scaling (MDS) ordination of ROV transects was constructed from a Bray-Curtis similarity matrix of square root transformed fish densities. A square root transformation was used to reduce the disparity between uncommon and abundant species by downweighting abundant species relative to uncommon species (Clarke, 1993). Prior to analyses, transects in which no fishes were observed were deleted, as the same reason may not apply to why two samples are devoid of species. Species comprising <0.01% of the total abundance of fish were also removed to minimize rare species confounding the cluster analysis. All pelagic species were removed from PRIMER analyses because we wanted to focus on benthic fish species associated with reef habitat. A two-way crossed analysis of similarity (ANOSIM) and pairwise comparisons were used to detect significant differences in fish assemblages among habitat types and management areas.

PRIMER was also used to examine biodiversity among habitats and management areas by calculating average taxonomic distinctness (*Δ*⁺). This statistic uses the taxonomic distance between every pair of species in a given assemblage as the basis for determining relative diversity (Clarke and Warwick, 1998). Unlike conventional diversity indices such as the Shannon-Weiner Index, *Δ*⁺ is independent of sampling effort. To calculate *Δ*⁺, a total list of species observed from ROV transects was used. The following taxonomic categories were utilized: species, genus, family, order, class, and phylum. Each of these represents a node in determining taxonomic distances between species pairs. This list along with fish density data were used to run a TAXDTEST which produces funnel plots where *Δ*⁺ is plotted in comparison with the mean and 95% confidence limits.

Densities of grouper were singled out for analysis because their declining abundances led the South Atlantic Fishery Management Council to establish the OECA. A generalized linear model (GLM) (Minitab 13.32, State College, PA) was used to test for significant differences in grouper densities among management areas and habitat types. Individual species of grouper were not abundant enough to analyze separately, so all grouper species were combined. One-way analysis of variance (ANOVA) was used to test for significant differences in grouper densities among management areas within each habitat type. A significance level of $P \leq 0.05$ was applied to all analyses, and log transformations were applied to correct for unequal variances. Pairwise comparisons were performed using Tukey's honestly significant differences (HSD).

Habitat quantification analyses

A digital still image of the seafloor (taken pointing straight down from the ROV, perpendicular to the seafloor) was taken every 1–3 min during ROV transects to quantify habitat type among management areas. These images were imported into an image analysis program written at the University of North Carolina-Wilmington, emulating the area/length analysis tool of Coral Point Count software (CPCe, Dania Beach, FL) (Kohler and Gill, 2006). Within each image, a polygon was drawn around each distinctive hardbottom area and a habitat type assigned to it. Habitat types were the same as those used for video analyses with the addition of human artifacts (e.g., fishing line, bottles) and shadow, where all or part of an image was blurred, usually from sand being stirred up by the ROV. The program then calculates the percentage of each habitat type within an image based on the number of pixels in each polygon. The area of each habitat type was calculated using paired lasers (set at a known distance of 10 cm apart) on each image. Mean area of still images was 1.2 m² ±0.05 m². One-way ANOVAs were then used to test for significant differences in habitat type percentages among management areas.

Results

Fish assessment

Forty-two ROV dives (65 hours of video footage) were completed in 2003 and 2005, resulting in 512 hardbottom 50-m transects: 236 in the OECA, 184 in the OHAPC, and 92 in the open area. Among habitat types, 72 transects were in pavement, 186 in rubble, 210 in rock outcrops, 11 in standing dead *O. varicosa*, and 33 in live *O. varicosa*. A total of 62 fish species were observed (Table 1). The previously unexplored bioherms discovered outside the OHAPC between the two satellite areas turned out to be comprised mostly of coral rubble, therefore, even though some live and standing dead *O. varicosa* were observed in the open areas, there wasn't enough of it to produce any 50-m transects to be used in the analyses. No fish species were exclusive to *O. varicosa* coral (live or standing dead). No grouper species were found on pavement except scamp (*Mycteroperca phenax*), the most abundant grouper. Tattlers (*Serranus phoebe*), one of the most abundant small sea basses were

Table 1

Relative abundance (%) of all fish species observed from remotely operated vehicle (ROV) transects on the Oculina Bank during April/May 2003 and October 2005. Species are listed by management area (open= any area outside the OHAPC open to fishing, OHAPC=areas where all bottom gear except hook and line are restricted, i.e., excluding the OECA, and OECA= inside the MPA where all bottom gear, including hook and line fishing, are restricted) and habitat (PAV=pavement, RUB=rubble, OUT=rock outcrops, SD=standing dead *Oculina*, LO=live *Oculina*). There were no SD or LO transects in the open area. A dash indicates 0.00% relative abundance.

	open			OHAPC					OECA				
	PAV	RUB	OUT	PAV	RUB	OUT	SD	LO	PAV	RUB	OUT	SD	LO
Muraenidae													
Gymnothorax spp.	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Undetermined	—	—	—	—	—	—	—	—	—	0.15	—	—	—
Ophicithidae													
Undetermined	—	—	—	—	—	—	—	—	—	—	0.10	—	0.14
Engraulidae													
Anchoa spp.	—	—	—	—	—	—	—	—	—	7.14	—	—	0.28
Synodontidae													
Synodus intermedius	—	—	—	—	0.13	—	—	—	1.49	—	—	—	0.15
Synodus spp.	—	—	—	—	0.14	0.15	—	—	0.76	—	—	—	—
Ogcocephalidae													
Ogcocephalus corniger	—	—	0.12	—	—	—	—	—	—	0.07	—	—	—
Ogcocephalus spp.	—	0.20	—	—	—	—	—	—	—	—	—	—	—
Holocentridae													
Holocentrus rufus	—	—	0.27	—	—	0.38	—	—	—	—	—	—	—
Holocentrus spp.	—	—	—	—	—	—	—	—	—	0.07	0.50	—	—
Myripristis jacobus	—	—	0.13	—	—	—	—	—	—	—	—	—	—
Syngnathidae													
Hippocampus spp.	—	—	—	—	0.14	0.15	—	—	2.34	—	0.50	—	—
Scorpaenidae													
Helicolenus dactylopterus	—	—	0.39	—	—	0.46	—	—	—	0.56	—	—	—
Undetermined	—	0.81	0.39	—	—	0.23	—	—	—	1.60	—	—	1.13
Triglidae													
Prionotus spp.	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Serranidae													
Anthiinae	—	—	3.30	—	11.24	9.06	30.85	25.22	—	16.80	45.22	—	43.79
Centropristis ocyurus	6.63	4.06	8.95	20.91	2.18	8.21	8.29	1.18	16.92	4.13	1.62	7.98	5.16
Centropristis spp.	—	39.93	11.68	38.02	4.52	14.04	4.97	1.19	9.70	3.53	3.15	14.27	5.76
Centropristis striata	—	—	0.12	5.91	—	—	0.83	—	12.26	1.03	0.80	—	0.43
Epinephelus adscensionis	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Epinephelus drummondhayi	—	—	—	—	—	—	—	—	—	—	0.09	—	0.14
Epinephelus morio	—	—	—	—	0.14	0.31	—	—	—	0.07	0.10	2.23	0.28
Epinephelus niveatus	—	—	0.13	—	—	0.15	—	—	—	—	0.19	—	0.14
Hemanthias vivanus	—	5.13	6.69	—	3.00	5.26	3.31	3.41	—	2.21	4.81	—	—
Liopropoma eukrines	—	—	1.93	—	0.42	0.76	0.81	—	—	0.14	1.35	—	1.16
Pronotogrammus martinicensis	—	8.02	31.47	—	17.49	18.74	15.53	13.33	—	4.92	8.55	—	0.14
Mycteroperca microlepis	—	—	—	—	—	0.08	—	—	—	—	—	—	—
Mycteroperca phenax	—	0.20	0.90	2.97	0.13	1.13	4.89	1.76	0.46	0.58	1.59	2.16	1.70
Mycteroperca spp.	—	0.20	—	—	—	—	—	—	—	—	—	—	—
Rypticus maculatus	—	—	—	—	—	—	—	—	—	0.14	—	—	—
Serranus annularis	—	0.20	0.25	—	0.28	—	—	—	—	0.07	—	—	—
Serranus notospilus	—	5.16	0.64	1.00	1.67	1.37	3.30	0.57	1.24	0.40	—	—	0.86
Serranus phoebe	60.57	13.16	10.17	17.74	13.51	16.92	7.53	1.79	27.14	14.91	8.67	14.33	5.16

Table 1 (continued)

	open			OHAPC					OECA				
	PAV	RUB	OUT	PAV	RUB	OUT	SD	LO	PAV	RUB	OUT	SD	LO
Anthiinae (cont.)													
Serranus spp.	—	0.42	0.12	—	—	0.22	—	—	—	0.36	—	—	—
Serranus subligarius	—	—	—	—	—	—	—	—	—	0.36	—	—	0.71
Undetermined grouper	—	—	—	—	—	0.08	—	0.59	0.93	—	0.20	—	0.15
Undetermined small sea bass	—	0.60	0.13	1.02	0.97	0.29	4.19	1.17	2.54	0.11	—	—	—
Priacanthidae													
Priacanthus arenatus	—	—	0.26	—	—	0.74	—	—	—	—	0.57	—	—
Pristigenys alta	13.20	0.20	1.93	3.93	—	4.27	—	—	6.79	0.60	4.47	1.15	0.28
Undetermined	—	—	—	—	—	0.23	—	—	—	—	—	—	—
Apogonidae													
Apogon pseudomaculatus	—	—	—	0.94	—	0.43	—	—	0.94	0.07	0.10	1.09	1.32
Apogon spp.	—	—	0.39	—	—	1.28	—	—	—	0.36	1.07	1.17	0.86
Rachycentridae													
Rachycentron canadum	—	—	—	—	—	0.15	—	—	—	—	—	—	—
Carangidae													
Seriola dumerili	—	—	0.50	—	—	0.79	1.62	—	0.93	0.42	0.29	—	—
Seriola rivoliana	—	—	—	—	0.27	—	—	—	—	—	—	—	—
Seriola spp.	6.91	—	0.13	—	0.41	0.40	—	—	0.47	0.29	0.40	—	0.14
Seriola zonata	—	—	0.13	—	—	—	—	—	0.49	0.14	—	—	—
Lutjanidae													
Lutjanus campechanus	—	—	—	—	—	0.08	—	—	—	—	—	—	—
Lutjanus spp.	—	—	0.13	—	—	—	—	—	—	—	—	—	—
Ocyurus chrysurus	—	—	—	—	—	—	—	—	—	0.08	—	—	—
Haemulidae													
Haemulon aurolineatum	—	—	—	—	—	—	—	—	—	5.03	—	—	—
Haemulon spp.	—	—	—	—	—	—	—	—	—	1.43	—	—	—
Sparidae													
Pagrus pagrus	—	—	0.37	—	—	—	—	—	—	0.14	0.10	—	—
Undetermined	12.69	—	0.13	—	—	0.12	—	—	1.43	0.36	0.39	—	0.42
Sciaenidae													
Equetus acuminatus	—	—	—	0.98	0.14	—	—	—	—	0.49	—	—	—
Equetus spp.	—	—	0.13	—	—	—	—	—	—	—	—	—	—
Equetus umbrosus	—	—	—	—	—	—	—	—	—	—	0.10	—	3.56
Micropogonias undulatus	—	—	—	—	—	—	—	—	—	0.18	—	—	—
Pareques iwamotoi	—	—	—	1.97	—	0.30	—	—	—	—	—	—	—
Chaetondontidae													
Prognathodes aya	—	1.43	2.95	—	2.49	1.66	4.95	2.96	—	7.53	4.02	3.22	10.06
Chaetodon ocellatus	—	—	0.27	—	—	0.15	—	1.74	—	0.07	0.49	—	—
Chaetodon sedentarius	—	0.39	1.04	—	1.65	0.90	—	1.00	—	1.66	1.27	—	0.56
Chaetodon spp.	—	—	0.25	—	0.27	0.08	—	0.59	—	0.79	—	—	—
Pomacanthidae													
Holacanthus bermudensis	—	—	0.66	—	—	0.22	2.44	2.34	—	0.43	1.00	2.13	0.70
Holacanthus ciliaris	—	—	—	—	—	0.07	—	—	—	—	—	—	—
Holacanthus spp.	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Pomacentridae													
Chromis enchrysurus	—	12.32	7.60	—	36.71	5.66	5.68	29.27	8.01	17.56	5.93	44.43	12.55
Chromis scotti	—	0.85	—	—	—	—	—	—	—	0.14	—	—	—
Chromis spp.	—	0.20	0.14	—	0.14	—	—	0.61	—	0.08	—	—	—
Microspathodon chrysurus	—	—	—	—	—	—	—	—	—	0.37	—	—	—
Labridae													
Bodianus pulchellus	—	—	—	—	—	0.15	—	—	—	0.07	0.19	—	—
Bodianus rufus	—	—	—	—	—	—	—	—	—	0.14	—	—	—
Decodon puellaris	—	—	0.12	—	—	0.15	—	—	—	0.07	0.26	5.83	0.14
Halichoeres bathyphilus	—	0.21	—	—	—	—	—	—	—	0.30	—	—	—
Halichoeres spp.	—	3.22	4.45	—	1.54	3.06	—	2.29	—	0.28	1.29	—	0.70

Table 1 (continued)

	open			OHAPC					OECA				
	PAV	RUB	OUT	PAV	RUB	OUT	SD	LO	PAV	RUB	OUT	SD	LO
Sphyraenidae													
Sphyraena barracuda	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Bothidae													
Cyclopsetta fimbriata	—	—	—	—	—	—	—	—	—	—	—	—	0.14
Undetermined	—	—	0.14	0.98	—	—	0.83	—	2.44	—	0.10	—	0.29
Balistidae													
Balistes capriscus	—	—	—	—	—	—	—	—	—	—	0.10	—	—
Monacanthidae													
Aluterus monoceros	—	—	—	—	—	—	—	—	—	0.07	—	—	—
Stephanolepis hispidus	—	—	—	—	—	0.07	—	—	—	—	0.10	—	—
Monacanthus spp.	—	—	—	—	—	0.19	—	—	—	0.07	—	—	—
Ostraciidae													
Lactophrys quadricornis	—	—	—	—	—	—	—	—	—	0.21	—	—	—
Lactophrys spp.	—	—	—	—	—	—	—	—	—	—	0.17	—	—
Tetraodontidae													
Sphoeroides spengleri	—	2.88	0.51	3.62	0.41	0.42	—	—	2.72	0.83	0.16	—	0.44
Sphoeroides spp.	—	—	—	—	—	0.34	—	—	—	0.07	—	—	0.57
Diodontidae													
Chilomycterus spp.	—	0.20	—	—	—	—	—	—	—	—	—	—	—

found in every habitat and management area. Rock hind (*Epinephelus adscensionis*), speckled hind (*E. drummondhayi*), grey triggerfish (*Balistes capriscus*), and grunts (family Haemulidae) were only observed in the OECA.

Multivariate analyses based on 39 fish species across 473 transects indicated no differences in fish assemblages among hardbottom habitat types or management areas. MDS ordination portrayed a potentially useful representation of relationships among ROV transects in two-dimensional space (stress=0.2; see Clarke and Warwick, 2001) and showed no distinct groupings (Fig. 2). ANOSIM results confirmed these conclusions, fish assemblages were not significantly different among hardbottom habitat types (ANOSIM, Global R=0.128, *P*=0.001) or management areas (ANOSIM, global *R*=0.061, *P*=0.002). For ANOSIM, the *P* value is highly sensitive to sample number and, therefore, the likelihood of committing a type-I error is high. For that reason, the *R* value is more important than the *P* value. *R* equals 0 when groups are the same and *R* equals 1 when groups are different (Clarke and Warwick, 2001).

Among habitat types, species richness was highest on rock outcrops and lowest for standing dead *O. varicosa* (Fig. 3). Average taxonomic distinctness (Δ^+) was
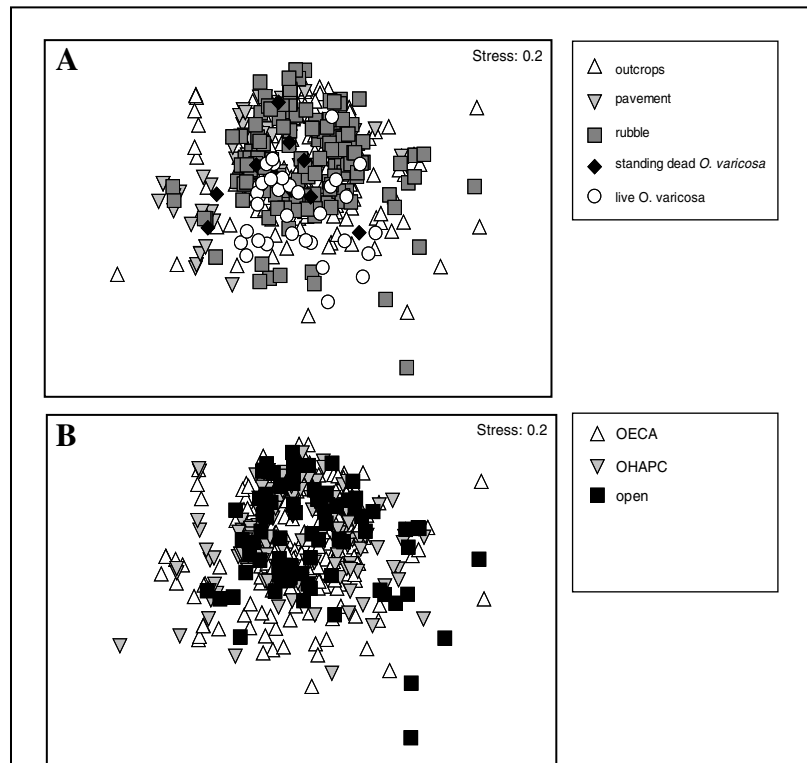

Figure 2
Multidimensional scaling (MDS) ordination of habitats (**A**) and management areas (**B**) based on the Bray-Curtis similarity matrix calculated from square root transformed fish densities (39 species). Data were collected from remotely operated vehicle (ROV) transects conducted on the Oculina Bank during April-May 2003 and October 2005.

highest for rock outcrops followed by pavement, rubble, and live *O. varicosa*, all of which were within the 95% confidence limits. Species richness (*Δ*⁺) for standing dead habitat, however, was less than expected and fell below the 95% confidence limits. Among management areas, species richness was higher in the OECA and OHAPC compared to the open management area (Figure 3). Average taxonomic distinctness (*Δ*⁺) for the OECA and OHAPC were within the 95% confidence limits, however, *Δ*⁺ for the open area was less than expected falling below the 95% confidence limits.

Grouper densities were significantly different among habitat types (GLM, *P*<0.001) and management areas (GLM, *P*=0.033) (Fig. 4). Observed grouper species include speckled hind, red grouper (*E. morio*), snowy grouper (*E. niveatus*), scamp, gag (*M. microlepis*), and rock hind (*E. adscensionis*). Pairwise comparisons revealed that grouper densities were significantly higher (*P*<0.05) on live *O. varicosa*, rock outcrops, and standing dead *O. varicosa* compared to pavement and rubble. Grouper densities were also higher in the OECA compared to both the OHAPC and open management areas. When compared within each single habitat, grouper densities were significantly different on rock outcrops (One-way ANOVA, *P*=0.023) and pairwise comparisons revealed that densities were higher in the OECA compared to both the OHAPC and open areas (*P*<0.05). Grouper densities among management areas were not significantly different (*P*>0.05) for any of the other habitat types.

Habitat assessment

Analysis of digital stills revealed the highest percentage of live coral habitat was found in the OECA making up only 1.9% of the total habitat observed (Fig. 5). A total of 1307 digital still images were taken in 2003 and 2005 and used for analysis. There was significantly more live *O. varicosa* located within the OECA compared to the OHAPC and open (One-way ANOVA, *P*=0.025). The percentage of rock outcrops was significantly higher in the OHAPC compared to the open and OECA as well as in the open compared to the OECA (One-way ANOVA, *P*<0.001). Significantly more rubble was found in the OECA and open compared to the OHAPC (One-way ANOVA, *P*<0.001). The percentage of pavement was significantly higher in the OECA and OHAPC compared to the open area (One-way ANOVA, *P*=0.003) and, finally, there was significantly more standing dead *O. varicosa* in the OECA than the open (One-way ANOVA, *P*=0.032). Location of video transects and digital still images containing live *O. varicosa* are shown in Figure 6.

Discussion

This is the first study to address the functionality of coral habitat and to compare fish assemblages among areas with different management levels on the Oculina Bank. Prior to this study, the last survey conducted on the Oculina Bank was in 2001 (Koenig et al., 2005), however, several differences exist between the two and new findings have emerged from the current survey. Koenig et al. (2005) targeted high relief sites within the OECA, used side-scan sonar to locate sites, and compared fish densities among three general habitat types (no coral, sparse live and dead *O. varicosa*, and dense live and dead *O. varicosa*). The current study had updated multibeam maps to target sites,

Figure 3

Average taxonomic distinctness (*Δ*⁺) of fish assemblages relative to the mean *Δ*⁺ (dashed line) and the 95% confidence intervals (solid lines) by habitat (**A**) and management area (open = any area outside the OHAPC open to fishing, OHAPC = areas where all bottom gear except hook and line are restricted, i.e., excluding the OECA, and OECA = inside the MPA where all bottom gear, including hook and line fishing, are restricted) (**B**) from remotely operated vehicle (ROV) transects conducted on the Oculina Bank during April–May 2003 and October 2005.

compared areas not only within the OECA but also included the OHAPC and open areas, and examined an expanded range of habitats.

While it is well known that deep coral habitat supports a high diversity and densities of fish species (Costello et al., 2005; Koenig et al., 2005; Parrish, 2006; Stone, 2006; Ross and Quattrini, 2007), it is unclear whether fish are attracted to live coral or just structure made by corals. Our study addressed this question by comparing fish assemblages, densities, and diversity among several structure-forming habitat types including coral. We found no significant difference in the composition of fish assemblages or diversity among all hardbottom habitat types. Grouper densities were significantly higher on the most structurally complex habitats (live *O. varicosa*, standing dead *O. varicosa*, and rock outcrops) compared to the less complex ones (pavement and rubble). Therefore, higher grouper densities were not exclusive to coral habitats. According to Auster (2005), one of the ways to define functionally equivalent habitats is those that support a similar density of fishes, therefore, we conclude that *O. varicosa* was functionally equivalent to the other hardbottom habitats on the Oculina Bank. Similar results were found in the Gulf of Maine (Auster, 2005). No difference in fish communities was found between habitats dominated by dense corals and those dominated by dense epifauna with or without corals. In addition, Tissot et al. (2006) concluded that fishes in southern California were associated with sponges and corals, but no functional relationship was present. In Hawaii, fish densities were higher in areas with deep-water corals, but when bottom relief and depth were accounted for, these densities were not higher than those for surrounding areas without corals (Parrish, 2006). Ross and Quattrini (2007) concluded that deep slope reefs function much like shallow corals reefs, hosting a unique, probably obligate, ichthyofauna, however other hardbottom habitats were not examined.

Even though our study demonstrated that *O. varicosa* serves a similar role for fishes as other hardbottom habitats, corals are still important and are major contributors to deep-sea habitat complexity and structure (Roberts et al., 2006). Significant numbers of gag and scamp aggregate on and use *O. varicosa* for spawning habitat and juvenile speckled hind use the coral for shelter suggesting a nursery value of the coral (Gilmore and Jones, 1992; Koenig et al., 2000; Koenig et al., 2005). Intact coral is not only valuable for fish, but invertebrates as well. As long as the coral is standing (live or dead), living space within the colony branches supports dense and diverse communities of associated invertebrates (Reed et al., 2002a, 2002b; Reed et al., 2007). However, once reduced to unconsolidated coral rubble, little living
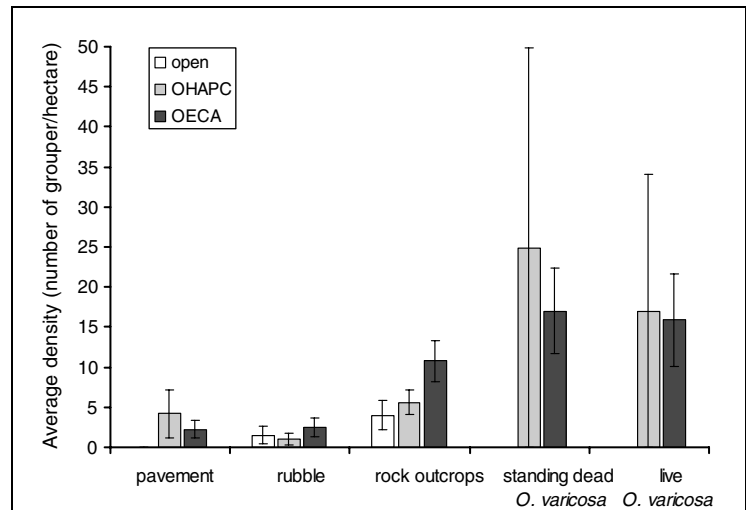

Figure 4

Average grouper densities (no./hectare) (±SE) for each management area by habitat type observed from remotely operated vehicle (ROV) transects conducted on the Oculina Bank during April/May 2003 and October 2005. Average grouper density for pavement in the open area was 0.0 fish/hectare, however, there were no live or standing dead *Oculina varicosa* transects for the open area.
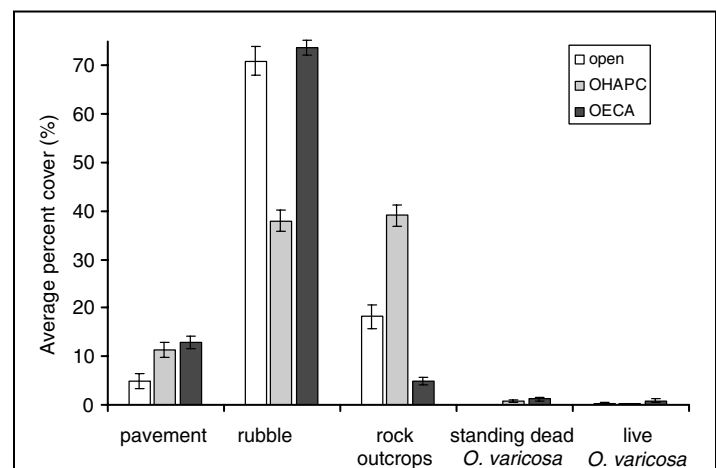

Figure 5

Average percent cover (±S.E.) of habitat types in each of the three management areas (open = any area outside the OHAPC open to fishing, OHAPC = areas where all bottom gear except hook and line are restricted, i.e., excluding the OECA, and OECA = inside the MPA where all bottom gear, including hook and line fishing, are restricted) from analysis of digital stills taken during remotely operated vehicle (ROV) transects on the Oculina Bank during April–May 2003 and October 2005.

space is left except for infauna (George et al., 2007). A hypothetical trophic model of the *O. varicosa* ecosystem indicates significant loss of habitat, in particular intact

live and dead standing coral, could bring dramatic shifts in the ecosystem (George et al., 2007). Conservation efforts, however, should focus on the intrinsic value of corals such as their slow growth, high sensitivity to disturbance, and questionable potential for recovery (Auster, 2005). A restoration project utilizing artificial reef structures is currently ongoing within the OECA. Between 1996 and 2001, a total of 125 large and 900 small restoration modules were deployed in a series of experiments to test their efficacy in the recovery of degraded coral and depleted fish populations (Koenig et al, 2005). The theory is that this will help *O. varicosa* restoration by providing stable settlement habitat, which may, in turn, provide suitable habitat for fish populations to recover. Early evidence (ROV dives from this study) found new coral recruits growing on the structures and groupers associated with them as well (Reed et al., 2005). While the scale of the artificial reefs is likely too small for fisheries replenishment, this experiment will provide insight to whether this tool is effective for coral restoration.

Being the first study to compare fish assemblages among areas with different management levels on the Oculina Bank, the results are important to the South Atlantic Fishery Management Council as they evaluate the effectiveness of the OECA; this study and future surveys will help determine the fate of the closed area when it is reconsidered by the Coral and Habitat Advisory Panels in 2014. While MDS and ANOSIM analyses revealed no significant differences in the composition of fish assemblages among management areas, other positive effects of the closure were observed. Fish diversity was higher inside the OHAPC and OECA compared to the open area. Grouper densities were significantly higher in the OECA, particularly on rock outcrops, than in the OHAPC or open areas. Also, more coral was found in the OECA suggesting the restriction of fishing activity may have aided in conserving what little *O. varicosa* had not been destroyed by trawling. Habitat quantification analyses demonstrated there was significantly more live and standing dead *O. varicosa* in the OECA compared to the OHAPC and open.

An important observation from the ROV transects was the presence of black sea bass (*Centropristis striata*) in 2005. Prior to that time, black sea bass had not been observed on the *O. varicosa* reefs since the 1980s when they dominated the area (Koenig et al., 2000). While black sea bass in the 1980s were large, mature individuals, most individuals in 2005 were small juveniles, ranging in length from 10 to 20 cm, suggesting initial stages of recovery for this species. Another significant discovery was the sighting of the first juvenile speckled hinds since the 1980s. All of these findings combined present initial evidence demonstrating effectiveness of the MPA for restoring reef fish and their habitat.

Sustained enforcement remains an ongoing problem for MPAs (Riedmiller and Carter, 2001; Rogers and Beets, 2001). Even relatively moderate levels of poaching can quickly deplete gains achieved by closure (Roberts and Polunin, 1991; Russ and Alcala, 1996). As of 2003, all trawling vessels working in the Oculina Bank area are required to have vessel monitoring systems, but this doesn't solve the problem of poaching by hook and line fishing. Between 2003 and 2007, illegal trawlers and fishers were observed within the MPA during our cruises, and several vessels have been cited and fined by the United States Coast Guard. ROV observations from this study indicate recent trawl nets, bottom long lines, and fishing lines inside the MPA long after these gears were banned from the area. Continued trawling and bottom fishing in the OHAPC likely will thwart management objectives.
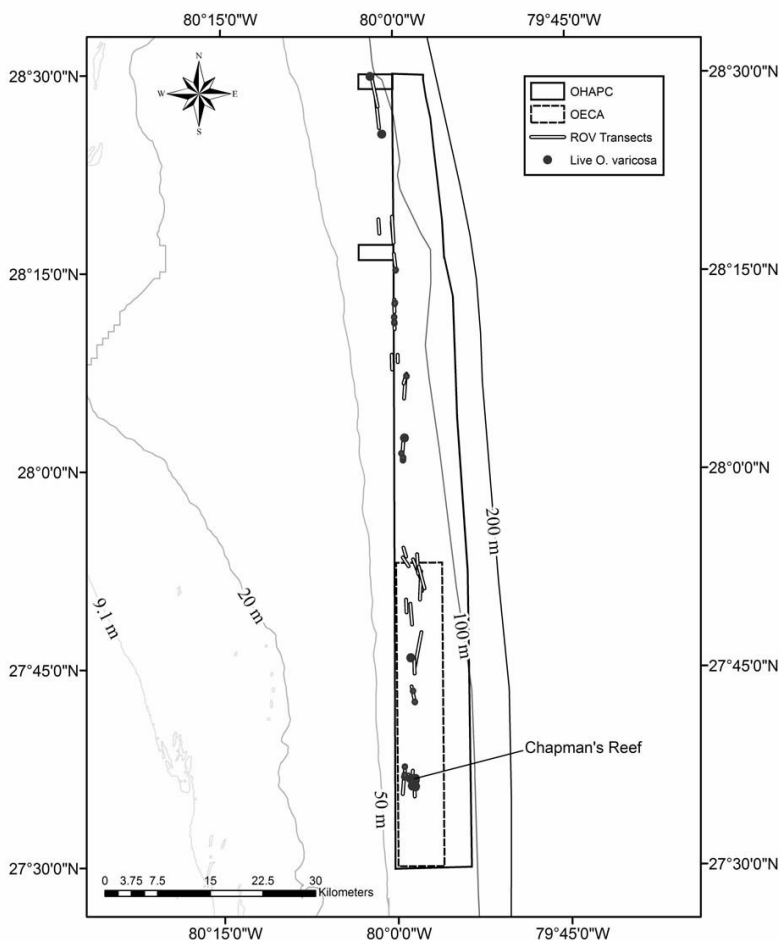

Figure 6

Locations of live *Oculina varicosa* (ivory tree coral) from video and digital stills collected during remotely operated vehicle (ROV) transects during April–May 2003 and October 2005.

In summary, unlike shallow-water ecosystems, understanding of the ecological and functional role of deep-water corals has only recently emerged. The current study is in agreement with most other recent literature, demonstrating that corals are functionally equivalent to other deep-sea structural habitats. Deep-sea corals, however, are clearly an important provider of structural habitat for fishes and are sensitive to fishing gear impacts and vulnerable to destruction due to their fragility and slow growth rates. Therefore, protection remains crucial. While an ecosystem approach to management has become widely accepted and MPAs have become a primary tool to manage deep-sea coral ecosystems, little evidence has been provided demonstrating MPA effectiveness. This study, however, revealed several positive effects of the closure including higher biodiversity, grouper densities, and percentage of intact coral suggesting initial effectiveness of the *Oculina* MPA.

Acknowledgments

Literature cited

Allison, G. W., J. Lubchenco, and M. H. Carr.
  1998.   Marine reserves are necessary but not sufficient for marine conservation.   Ecol. Appl. 8:S79–S92.

Auster, P. J.
  2005.   Are deep-water corals important habitats for fishes? *In* Cold-water corals and ecosystems (A. Freiwald and J. M. Roberts, eds.), p. 747–760.   Springer, Berlin, Heidelberg.

Avent, R. M., M. E. King, and R. H. Gore.
  1977.   Topographic and faunal studies of shelf-edge prominences off the central eastern Florida coast.   Hydrobiol. 62(2):185–208.

Bohnsack, J. A.
  1998.   Application of marine reserves to reef fisheries management.   Aust. J. Ecol. 23:298–304.

Clarke, K. R.
  1993.   Non-parametric multivariate analyses of changes in community structure.   Aust. J. Ecol. 18:117–143.

Clarke, K. R. and R. M. Warwick.
  1998.   A taxonomic distinctness index and its statistical properties.   J. Appl. Ecol. 35:523–531.
  2001.   Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed.   PRIMER-E, Plymouth, U.K.

Costello, M. J. M. McCrea, A. Freiwald, T. Lundälv, L. Jonsson, B. J. Bett, T. C. E. van Weering, H. de Haas, J. M. Roberts, and D. Allen.
  2005.   Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic.   *In* Cold-water corals and ecosystems (A. Friewald and J. M. Roberts, eds.), p. 771–805.   Springer-Verlag, Berlin, Heidelberg.

Fosså, J., P. Mortensen, and D. Furevik.
  2002.   The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts.   Hydrobiol. 471:1–12.

George, R. Y., T. A. Okey, J. K. Reed, and R. P. Stone.
  2007.   Ecosystem-based fisheries management of seamount and deep-sea coral reefs in U. S. waters: conceptual models for proactive decisions.   *In* Conservation and adaptive management of seamounts and deep-sea coral ecosystems (R. Y. George and S. D. Cairns, eds.), p. 9–30.   Rosentiel School of Marine Science and Atmospheric Science, Univ. Miami, Miami, FL.

Gilmore, R. G. and R. S. Jones.
  1992.   Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain.   Bull. Mar. Sci. 51(1):83–103.

Guenette, S., T. Lauck, and C. Clark.
  1998.   Marine reserves; from Beverton and Holt to the present.   Rev. Fish Biol. Fish. 8:251–272.

Husebo, Å., L. Nottestad, J. H. Fosså, D. M. Furevik, and S. B. Jorgensen.
  2002.   Distribution and abundance of fish in deep coral habitats.   Hydrobiol. 471:91–99.

Jonsson, L. G., P. G. Nilsson, F. Floruta, and T. Lundaelv.
  2004.   Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast.   Mar. Ecol. Prog. Ser. 284:163–171.

Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace.
  2000.   Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reef of Florida.   Bull. Mar. Sci. 66(3):593–616.

Koenig, C.C., A. N. Shepard, J. K. Reed, S. D. Brooke, J. Brusher, and K. M. Scanlon.
  2005.   Habitat and fish populations in the deep-sea *Oculina* coral ecosystem of the western Atlantic.   Am. Fish. Soc. Sym. 41:795–805.

Kohler, K. E. and S. M. Gill.
  2006.   Coral point count with Excel extensions (CPCe): a visual Basic program for the determination of coral and substrate coverage using random point count methodology.   Computers and Geosciences 32(9):1259–1269.

Koslow, J. A., G. W. Boehlert, J. D. M. Gordon, R. L. Haedrich, P. Lorance, and N. Parin.
  2000.   Continental slope and deep sea fisheries: implications for a fragile ecosystem.   ICES J. Mar. Sci. 57:548–557.

Parrish, F. A.
  2006.   Precocious corals and subphotic fish assemblages.   Atoll Res. Bull. 543:425–438.

Pyle, R. L.
    2000.   Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology.   Mar. Tech. Soc. J. 34:82–91.
Reed, J. K.
    1980.   Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida.   Bull. Mar. Sci. 30(3):667–677.
    2002a.   Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management.   Hydrobiol. 471:43–55.
    2002b.   Comparison of deep-water coral reefs and lithoherms off southeastern USA.   Hydrobiol. 471:57–69.
Reed, J. K., C. C. Koenig, and A. N. Shepard.
    2007.   Impacts of bottom trawling on a deep-water *Oculina* coral ecosystem off Florida.   Bull. Mar. Sci. 81:481–496.
Reed, J. K., A. N. Shepard, C. C. Koenig, K. M. Scanlon, and R. G. Gilmore Jr.
    2005.   Mapping, habitat characterization, and fish surveys of the deep-water *Oculina* coral reef marine protected area: a review of historical and current research.   *In* Cold-water corals and ecosystems: proceedings of the second international symposium on deep sea corals (A. Freiwald, J. Roberts, eds.), p. 443–465.   Springer-Verlag, Berlin Heidelberg.
Riedmiller, S. and E. Carter.
    2001.   The political challenge of private sector management of marine protected areas: The Chumbe Island Case, Tanzania.   ACP-EU Fish. Res. Rep. no. 10, p. 141–153.
Roberts, C. M.
    2002.   Deep impact: the rising toll of fishing in the deep sea.   Trends Ecol. Evol. 17:242–245.

Roberts, C. M. and N. V. C. Polunin.
    1991.   Are marine reserves effective in management of reef fisheries?   Rev. Fish Biol. Fish. 1:65–91.
Roberts, J. M., A. J. Wheeler, and A. Friewald.
    2006.   Reefs of the deep: the biology and geology of cold-water coral ecosystems.   Science 312:543–547.
Rogers, C. S. and J. Beets
    2001.   Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands.   Environ. Conserv. 28(4):312–322.
Ross, S. W. and A. M. Quattrini.
    2007.   The fish fauna associated with deep coral banks off the southeastern United States.   Deep-Sea Research I. 54:975–1007.
Russ, G. R. and A. C. Alcala.
    1996.   Marine reserves: rate and patterns of recovery and decline of large predatory fish.   Ecol. Appl. 6:947–961.
Stone, R. P.
    2006.   Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions.   Coral Reefs 25:229–238.
Tissot, B. N., M. M. Yoklavich, M. S. Love, K. York, and M. Amend.
    2006.   Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral.   Fish. Bull. 104:167–181.
Watling, L. and E. A. Norse.
    1998.   Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting.   Conserv. Biol. 12(6):1180–1197.