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Habitat and Fish Populations in the Deep-Sea *Oculina* Coral Ecosystem of the Western Atlantic

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Abstract. The growth form of the scleractinian ivory tree coral *Oculina varicosa* (also known as fused ivory tree coral) that occurs on the shelf edge off Florida's eastern coast is unique for this species. Here, the branching coral colonies coalesce into thickets supporting high vertebrate and invertebrate biodiversity and high densities of economically important reef fish. In 1984, the South Atlantic Fishery Management Council took the first step to protect the area from trawling and other disruptive bottom activities. Despite these protective measures, however, there is evidence that trawling has damaged previously intact coral habitat. In this paper, we describe results from mapping studies conducted in 2001 and improvements to reef fish populations that have occurred in the last few years. We find that less than 10% of the area contains intact *Oculina* coral thickets, which we continue to attribute primarily to trawling. In addition, we find increased grouper density and male abundance inside the protected area, suggesting population recovery, and the appearance of juvenile speckled hind *Epinephelus drummondhayi* (family Serranidae), suggesting nursery function for this and possibly other commercially important species.

Introduction

Deep-sea coral species are subject to both increased interest and increased pressure (Malakoff 2003). The ivory tree coral *Oculina varicosa* (also known as fused ivory tree coral) is a case in point. This species, common in

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small (<30 cm), isolated, shallow water (2–30 m) colonies from the West Indies to North Carolina and Bermuda, occurs off Florida's eastern coast in deep (60–120 m), species-unique reefs as 2-m high azooxanthellate thickets on the slopes and crests of pinnacles (Reed et al. 1982; Reed 2002). These reefs, the *Oculina* Banks, extend 67 km along the outer shelf (Avent et al. 1977; Virden et al. 1996; Figure 1). Healthy *Oculina* reefs support a diverse invertebrate assemblage (Reed et al. 1982; Reed 2002), dense populations of fishes (G. Gilmore, Dynamac Corporation, Kennedy Space Center, unpublished data), and important spawning sites for many economically important reef fish species (Gilmore and Jones 1992; Koenig et al. 2000).

Interest in these unique *Oculina* thickets set in motion a series of protective measures by the South Atlantic Fishery Management Council (SAFMC), starting in 1984 with the designation of the *Oculina* Habitat Area of Particular Concern (OHAPC; 316 km^2) to prohibit the use of bottom gear. In 1994, the area became the Experimental *Oculina* Research Reserve (EORR), extending the prohibition to bottom fishing for 10 years to explore the use of marine protected areas (MPAs). In 2000, the OHAPC was expanded to 1,029 km^2. More recently (2003), the EORR closure was extended indefinitely.

Our 1995 observations in the EORR confirmed previous findings by Reed (1980) of extensive coral rubble (Koenig et al. 2000). We also found trawl damage to coral habitat known to be intact 20 years earlier and severely reduced reef fish populations. Jeff's Reef, a small (4-ha) area in the southern EORR (Figure 1), appeared to be the only intact area, although the biomass and number of economically important fish were much lower than they had been in the 1970s. The objectives of this study were to estimate the relative proportion of intact and rubble *Oculina* habitat on high relief sites in the OHAPC based on knowledge that intact coral habitat occurred predominantly on high relief and to evaluate reef fish use of both natural and artificial structure in the EORR.

Methods

The data presented here were derived from the National Oceanic and Atmospheric Administration's 2001 Islands in the Stream expedition. In 8 d (30 August–6 September), we completed 13 remotely operated vehicle (ROV) dives (Phantom S4, National Undersea Research Center, Wilmington, North Carolina) and 16 submersible dives (Clelia, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida) in the EORR and other portions of the OHAPC (Figure 1), producing more than 70 h of underwater videography. The ROV made line transects over large areas of the seafloor to determine the relative abundances of coral habitat on the ridges and pinnacles. The submersible made belt transects to quantify habitat type and fish density within habitat types.

Habitat Condition

We used a base map derived from side-scan sonar images (Scanlon et al. 1999) and the ship's echo sounder to set sampling sites. Collection site coordinates and transect lengths were determined with differential global positioning system navigation (Magnavox MX 200 global positioning system [GPS], accurate to within ± 5 m) and ArcView software. Plots of the submersible tracks and specific sample sites were made with the Integrated Mission Profiler (Florida Atlantic University, Boca Raton) linked to the ship's GPS.

Remotely Operating Vehicle Sampling

The ROV was tethered near the bottom to a 100-kg down weight by two parallel lines: (1) the first 20 m of the ROV umbilical, extending beyond the down weight to allow limited ROV movement at approximately 1.85 km/h (1.0 knot) northerly (i.e., with the Florida Current); and (2) a 19-m polypropylene tension-relief line to tow the ROV. The remaining ROV umbilical extended vertically to the vessel and was attached along its length. Transect positions were recorded while the ROV was under way to allow location of changes in geomorphology, habitat, and depth.

Manned Submersible Sampling

Habitat types identified by the ROV were further characterized by submersible with an underwater video (Insite-Tritech high sensitivity [0.0003 lux], high-resolution monochrome 1.23-cm charge coupled device). Video imagery on statistically random belt transects was recorded with laser-equipped downward-looking and forward-looking cameras. The downward-looking camera's two parallel lasers (25 cm apart) provided the scale for standardizing quadrat size and measuring coral colonies. The forward-looking camera's three inline lasers (10-cm intervals) provided the scale (two adjacent parallel beams) and distance (the third beam converged on the other two at 5 and 10 m), allowing determination of transect width at a selected distance from the camera. Laser dots were visible at approximately 5 m in the lower half of the camera's field of view.

Quadrats were derived from 16 to 20 randomly selected video frames from each downward-looking transect. Each quadrat was standardized relative to the laser metric and overlain with 100 randomly distributed dots to determine percent cover of each habitat type. The mean percent cover was calculated for each transect (averaging randomly selected frames) and compared within a given site for each habitat type using analysis of variance (ANOVA; arcsine transformation). A Shapiro–Wilk test for normality and Duncan's Multiple Range test were used to iden-

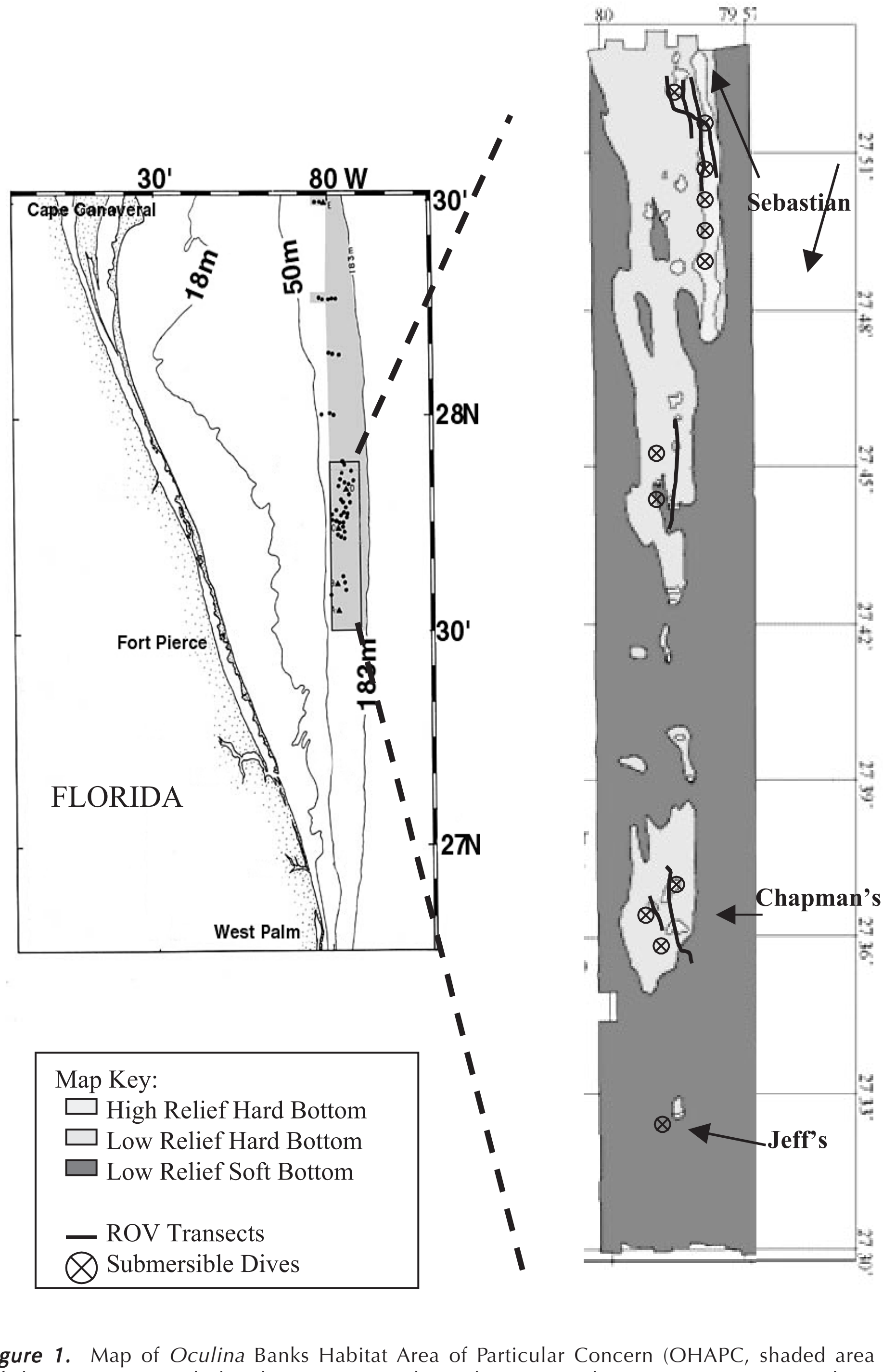

Figure 1. Map of *Oculina* Banks Habitat Area of Particular Concern (OHAPC, shaded area in left locator map), includes the Experimental *Oculina* Research Reserve (EORR, inset box on left, expanded on right). Dots in OHAPC are historic dive sites visited in the 1970s and 1980s. Expanded EORR shows hard and soft bottom, high and low relief (Scanlon et al. 1999), and location of 2001 remotely operated vehicle (ROV) transects and submersible dives.

tify homogeneous subsets among transect means. Randomly selected coral colonies within each transect were measured.

Fish Densities

Fish densities (numbers per ha) were determined during submersible belt transects in each habitat type. Transects were run without lights to avoid affecting fish behavior. Belt transect quantification of fish populations provides a statistical basis for spatial and temporal comparisons, measuring relative rather than absolute abundance and requiring that interannual comparisons account for temporal activity patterns.

Natural Habitat

Estimating belt transect area from submersible videos required determining the effective distance (D), the camera's horizontal angle of view ($A = 92°$), and the length (L) of the transect. The effective distance is the distance from the camera within which fish are counted and identified with high certainty rather than the limits of visibility (typically < 5 m, which was used as the standard distance; fish occurring beyond 5 m were excluded).

The field of view width (W) at distance D was calculated by:

$$W = 2\ [\tan\ (0.5A)]\ (D).$$

The area of the transect (TA) was calculated by:

$$\text{TA} = (L \times W) - 0.5(W \times D).$$

Estimating the transect area allowed calculating the average density and standard error of observed fish species within each habitat type. Species tending to follow or circle the submersible (e.g., greater amberjack and almaco jack) were *not* counted each time they appeared on the video. Rather, their total abundance was determined by observers in the submersible. Density differences among habitats were determined for numerically dominant species, economically important groupers, and pelagic species using ANOVA.

Habitat Modules

Reef balls (Reef Ball Foundation, *www.reefball.org*) (N = 105)—perforated concrete domes 1 m across and 0.7 m high—were deployed in 2000 to simulate the size and aspect of *Oculina* coral colonies and serve as larval recruitment surfaces, centers for *Oculina* thicket restoration through transplant growth, and structure replacement for reef fish (Figure 2; Koenig, Coleman, Brooke, and Brusher, unpublished data). They were distributed among nine areas (each 500 m^2) in clusters of 5, 10, or 20, with three replicates of each cluster size in a randomized block design to determine the most efficient density for attracting fish.

Results

Habitat Condition

Seven ROV line transects were made over high relief pinnacles and ridges in the EORR (Chapman's Reef: $N = 3$; Sebastian Reef: $N = 4$). Transect lengths ranged from 424 to 2,867 m, covering 7,645 m of high-relief seafloor (Figure 1). Three coral cover levels were identified: (1) dense—relatively undisturbed, large live and dead coral thickets with multi-scale structural complexity; (2) sparse—small colonies widely distributed in expanses of consolidated (rubble with identifiable coral branching) and unconsolidated rubble (fine coral debris), providing little structural complexity; and (3) no coral cover—sand, rock, and unconsolidated rubble, providing essentially no structural complexity. The relative proportion of each coral cover type was estimated as the proportional distance traversed by the ROV over that habitat type.

Of the total high relief pinnacle ridges transected, 464 m (6%) contained dense coral cover, 302 m (4%) contained sparse cover, and 6,877 m (90%) contained no cover. The only additional dense thickets identified during this study (Jeff's Reef having been located in 1995) were approximately 4 ha on the western bank of Chapman's Reef (Chapman's Reef West), one of three banks in Chapman's Reef (Figure 1). The only sparse habitats occurred on the south face of Chapman's Reef East and on the slope bases of Jeff's Reef and Chapman's Reef West. Three additional random transects covering 2,041 m of high relief just north of the EORR within the OHAPC revealed only unconsolidated rubble. Sparsely distributed, small (5–20-cm diameter) colonies of *Oculina* were associated with some of the rubble and with large boulders on low relief rocky bottom.

Sixteen belt transects were made in the EORR with the submersible ($N = 8$ at Jeff's Reef, $N = 5$ at Chapman's Reef West, $N = 3$ at Sebastian Reef; Figure 1), revealing four habitat types: intact live coral, intact dead coral, coral rubble, and bare rock and sand (Figure 3). Intact live coral only occurred on Jeff's Reef and Chapman's Reef West. Sebastian Reef was mostly coral rubble. Within each reef, the mean live coral coverage varied considerably among transects (ANOVA, $P < 0.01$). For Jeff's Reef, mean live coral coverage ranged from 9% to 21% and for Chapman's Reef West, 7% to 22% (Table 1). Coral colony diameter on Chapman's Reef West ranged from 8 to 143 cm, with a mean of 47.4 cm (SE = 4.75 cm, $N = 43$). Coral colony size on Jeff's Reef was not measured due to a laser malfunction.

Fish Populations

Natural Habitat

Population densities for the dominant fish species correlated highly with habitat type (Figure 4). Only one

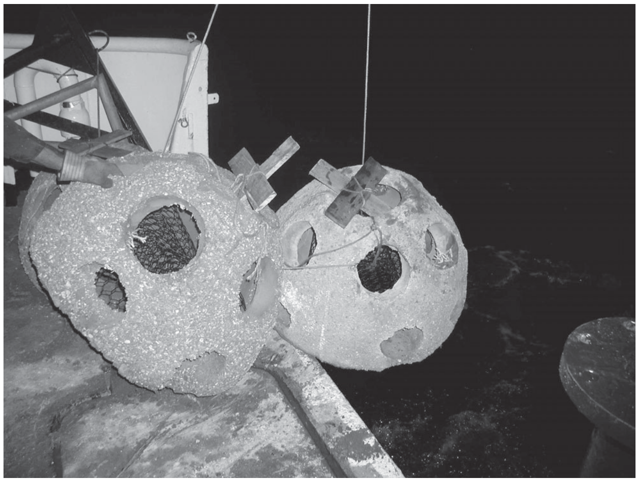

Figure 2. Habitat modules deployed on Sebastian Reef within the Experimental *Oculina Research Reserve* off the east coast of Florida in 2000. A wooden cross attached to the top of each reef ball with jute line (both substances being biodegradable) provided sufficient drag to make the reef balls land upright on the bottom.

economically important species was observed on coral rubble (Table 2). Highly cryptic juvenile speckled hind *Epinephelus drummondhayi* associated with intact habitat at average densities of 3–5 per ha. Male gag *Mycteroperca microlepis* occurred on Jeff's Reef.

Habitat Modules

Surveys of reef ball clusters occurred thirteen months after reef ball deployment. Surveys were easy to do because each cluster covered a small area (12.6-m radius). The mean species richness and abundance of economically important fish were greater for reef ball densities of 10 per cluster than for 5 but did not increase further at densities of 20 per cluster (Figure 5; Table 3). Male gag and scamp *Mycteroperca phenax* occurred near reef ball clusters.

Submersible observations around habitat modules and coral-transplant modules revealed module pieces missing and littering the bottom, suggesting impact by strong

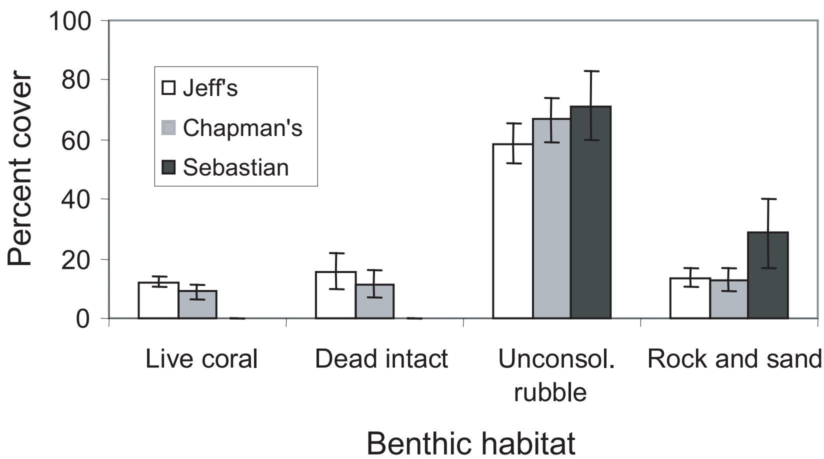

Figure 3. Percent cover of habitat types in intact coral habitat (Jeff's and Chapman's West Reef) and in unconsolidated rubble habitat (Sebastian Reef) within the Experimental *Oculina* Research Reserve off the eastern coast of Florida. Bars = standard error.

Table 1. Mean live coral cover and standing dead coral cover (in parentheses) determined from belt transects made with submersible on Jeff's Reef and Chapman's Reef in the *Oculina* Experimental Research Reserve. Thick horizontal lines indicate homogenous groupings of live coral (based on Duncan's multiple range test).

	Transect number							
Reef	1	2	3	4	5	6	7	8
Jeff's Reef	8.9 (8.4)	9.2 (3.2)	11.1 (17.7)	12.9 (8.4)	13.6 (7.4)	13.6 (10.4)	20.0 (46.2)	21.3 (49.8)
Chapman's Reef	7.0 (12.7)	7.7 (0)	9.2 (16.0)	11.0 (24.8)	22.3 (727.1)			

mechanical means. Apparent trawl tracks in the rubble were noted near the damage.

Discussion

Habitat Characterization

During this study, we specifically targeted high-relief sites in the OHAPC known in the 1970s to have either intact coral thickets (e.g., Jeff's Reef and Chapman's Reef) or extensive coral rubble (e.g., Sebastian Reef; Reed 1980; Koenig et al. 2000). We used direct observation rather than acoustic methods because the latter does not distinguish among live coral, dead intact coral, or unconsolidated rubble. Rubble is a major component on high-relief features. The concern is that so few high relief sites had intact thickets. Indeed, about 90% of the habitat surveyed was unconsolidated rubble; less than 10% contained intact coral colonies. No additional coral thickets were found within the EORR. Areas of the OHAPC north of the EORR known to contain thickets 20 years ago contained only coral rubble.

Ten percent intact coral on high relief features is likely a high estimate. If one assumes the EORR's only intact habitat is on Jeff's Reef and Chapman's Reef West, a lower estimate results. Roughly 3% (947 ha) of the EORR is high relief (Scanlon et al. 1999) and therefore suitable for *Oculina* thicket growth. With only 8 ha known to contain intact habitat, less than 1% of the intact habitat occurs on high relief sites. The more accurate estimate is likely somewhere in between. Although the ROV line transects targeted areas that once supported *Oculina* thickets, transposing old long-range navigation coordinates to GPS introduces uncertainty about historic site locations, and there was no way to anticipate which features would contain rubble and which would contain intact colonies.

In intact habitat, live coral coverage was less than half that of dead standing coral coverage, and both types of coverage were highly variable among transects. Observations of small coral colonies within coral rubble (primarily on high relief sites, occasionally on low relief sites) and extensive coral colonies on 60-year-old shipwrecks just outside of the EORR (M. Barnette, National Marine Fisheries Service, personal communication) suggest that coral colonization and growth occur but are insignificant. The presence of small dead standing colonies in low relief sites suggests that these may be marginal sites for survival.

Fish Populations

In the past 30 years, the size, age, and proportion of male gag and scamp have declined throughout the southeastern United States (Coleman et al. 1996; McGovern et al. 1998; Koenig et al. 2000). The results of this study suggest that protecting aggregation sites and resident populations within MPAs can help reestablish historical fish populations. Indeed, gag and scamp, including males, occur on coral thickets within the EORR but not on sites outside of the EORR. They also suggest some nursery function, based on the observation of juvenile speckled hind on Jeff's and Chapman's reefs. This is significant because the SAFMC considers this species threatened (Coleman et al. 2000). Density estimates of small fish or young individuals of typically larger species are probably low, especially in structurally complex habitats where these fish are often cryptic.

Unlike the typical artificial reef, which provides habitat and attracts reef fish to areas where neither previously existed, the reef ball modules replace destroyed habitat and serve as bases for reestablishing *Oculina* thickets. Observations thus far on restoration sites show promise only for reestablishing fish populations. All grouper species observed in 1980 on intact reefs (see Koenig et al. 2000), except warsaw grouper *Epinephelus nigritus*, associated with reef balls 1 year after their deployment. The reef balls may eventually support spawning, based on the presence of both gag and scamp males (typical of spawning aggregation sites, per Coleman et al. 1996), with scamp exhibiting presumed courtship behavior (described in Gilmore and Jones 1992).

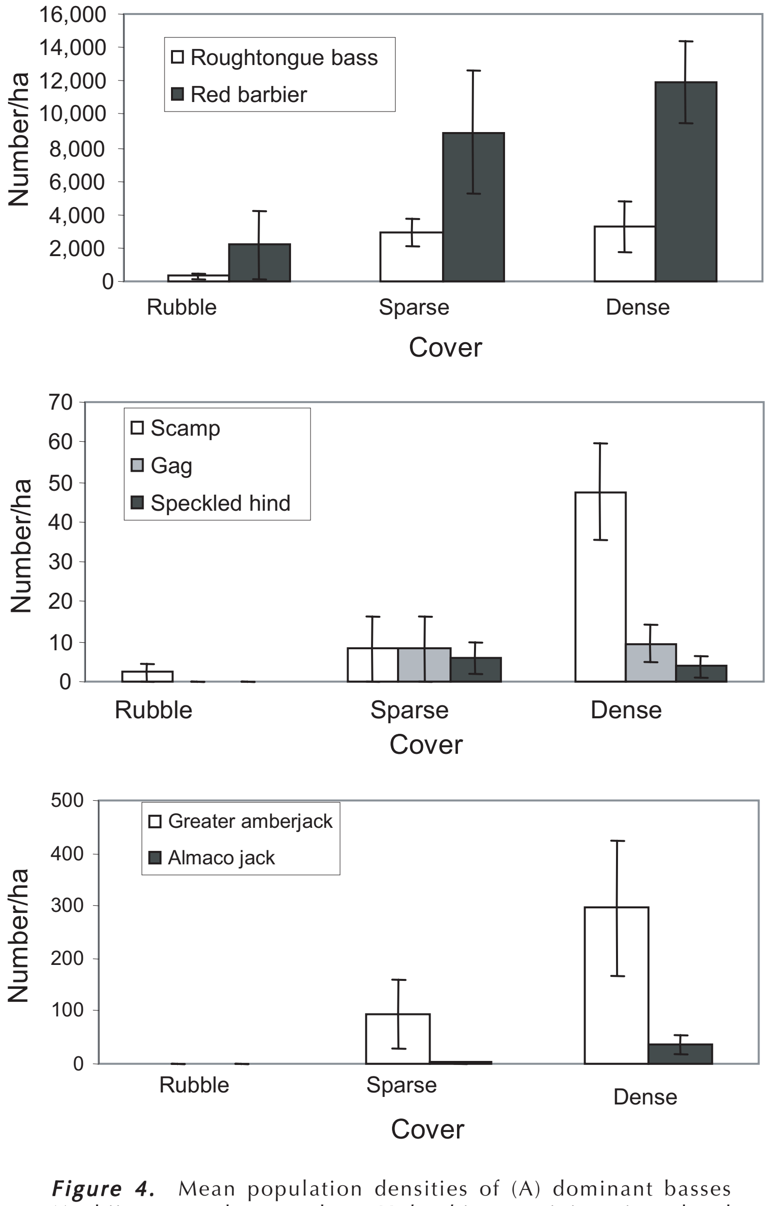

Figure 4. Mean population densities of (A) dominant basses (Anthiinae; roughtongue bass *Holanthias martinicensis* and red barbier *Hemanthias vivanus*), (B) dominant groupers (Epinephelinae; scamp, gag, and speckled hind), and (C) pelagic species (greater amberjack *Seriola dumerili* and almaco jack *S. rivoliana*) in three levels of coral habitat condition. Bars = standard errors. Scamp density in intact habitat was significantly greater ($P = 0.05$) than in other habitats.

Possible Causes of Habitat Decline

Natural, wholly unmanageable events that damage coral include extreme temperatures (Fitt et al. 2001), excessive nutrient input (Szmant 2002), strong currents (Lugo et al. 2000), and disease (Porter et al. 2001). *Oculina* is relatively tolerant of changes in temperature and nutrient and sediment input that occur during episodic deep-sea upwelling events (Reed 1983), although this tolerance may not persist in the face of global warming or increased nutrient loads associated with ocean dumping. Although no studies of

Table 2. Comparison of mean densities of species observed in intact habitat (Jeff's Reef and Chapman's Reef) and unconsolidated coral rubble (Sebastian Reef; presumably coral destroyed by trawling) within the Experimental *Oculina* Research Reserve. An asterisk indicates an economically important species.

	Jeff's Reef		Chapman's Reef		Sebastian Reef	
Species	Number/ha	SE	Number/ha	SE	Number/ha	SE
Red barbier	7,301	2,757	18,082	3,429	277	277
Roughtongue bass	1,211	410	6,424	3,560	141	89
Greater amberjack*	298	182	284	187		
Yellowtail reeffish *Chromis enchrysurus*	60	30	277	111	53	43
Almaco jack*	55	29				
Scamp*	48	11	47	27		
Blue angelfish *Holacanthus bermudensis*	39	13	204	72	6	6
Bank butterflyfish *Chaetodon aya*	27	10	110	35	19	12
Gag*	16	7				
Reef butterflyfish *Chaetodon sedentarius*	13	6	102	50	17	11
Specked hind*	3	3	5	5		
Tattler *Serranus phoebe*	3	3	27	12	44	12
Spotfin butterflyfish *Chaetodon ocellatus*	2	2				
Porgy *Calamus* spp.*			10	10		
Wrasse bass *Liopropoma eukrines*			17	13		
Soapfish *Rypticus* spp.			17	13		
Wrasse Labridae					42	26
Purple reeffish *Chromis scotti*			36	18		
Snapper *Lutjanus* spp.*					6	6

disease have been conducted in the *Oculina* banks, virulent pathogens would be expected to cause extensive damage to ahermatypic reefs like *Oculina* rather than selective elimination of some reefs but not adjacent reefs.

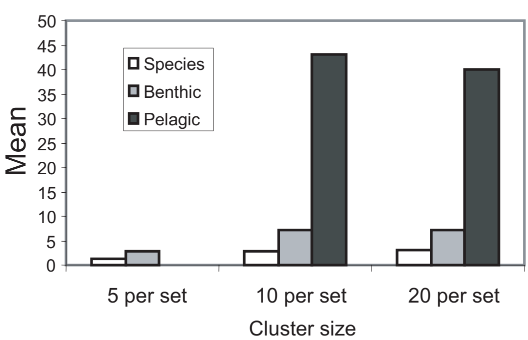

Figure 5. Mean number of species and individuals (benthic and pelagic) of economically important reef fish associated with three reef ball densities, 5 per 500 m^2, 10 per 500 m^2, and 20 per 500 m^2 set over unconsolidated coral rubble in Sebastian Reef within the Experimental *Oculina* Research Reserve off the east coast of Florida There were 3 replicates of each set.

Most of the evidence for *Oculina* habitat destruction points to human-induced impacts. While it is possible that World War II exchanges between U.S. and German vessels west of the OHAPC (Cremer 1986) caused some damage, these encounters ended about 60 years ago, allowing sufficient time for habitat recovery. Indeed, U.S. freighters sunk near the OHAPC by German U-boats in the 1940s support dense *Oculina* thickets on their decks (Barnette, personal communication).

Trawling continues to be the greatest manageable threat to the *Oculina* reefs (Koenig et al. 2000). Bottom trawling and dredging worldwide result in severe coral damage (Jones 1992; Rogers 1999; Fosså et al. 2000; Koslow et al. 2000; Richer de Forges et al. 2000), requiring long recovery times (Dayton et al. 2002; Johnson 2002). These have occurred off Florida's eastern coast for years, involving both foreign and domestic fleets. Foreign trawling stopped in the late 1970s with development of the U.S. Exclusive Economic Zone.

The extent to which domestic trawling persists in the *Oculina* banks is unknown. However, circumstantial evidence suggests that it does to some degree. Trawlable high relief bottom features where *Oculina* normally occurs show little evidence of coral recolonization, while

Table 3. Comparison of reef fish found on Sebastian Reef in the Oculina Experimental Research Reserve, associated with three different densities of reef balls deployed in coral restoration experiments. Asterisk indicated economically important species.

	5 reef balls/cluster		10 reef balls/cluster		20 reef balls/cluster	
Species	Number/1,500 m^2	%	Number/1,500 m^2	%	Number/1,500 m^2	%
Greater amberjack*			109	37.72		
Roughtongue bass	7	41.18	120	41.52	53	21.9
Red barbier			1	0.35	25	10.33
Almaco jack*			20	6.92	20	8.26
Scamp*	3	17.65	15	5.19	14	5.79
Wrasse			1	0.35	10	4.13
Blue angelfish			3	1.04	5	2.07
Reef butterflyfish			4	1.38	3	1.24
Red snapper*			6	2.08	2	0.83
Lutjanus campechanus						
Snowy grouper*	2	11.76			2	0.83
Epinephelus niveatus						
Speckled hind*					3	1.24
Tattler	1	5.88			2	0.83
Red porgy*	2	11.76			2	0.83
Pagrus pagrus						
Sharpnose puffer					1	0.41
Canthigaster rostrata						
Queen angelfish					1	0.41
Holacanthus ciliaris						
Bank butterfly	1	5.88	2	0.69		
Short bigeye			2	0.69		
Pristigenys alta						
Twospot cardinalfish			2	0.69		
Apogon pseudomaculatus						
Spinycheeck soldierfish			2	0.69		
Corniger spinosus						
Sharpnose puffer			1	0.35		
Canthigaster rostrata						
Bank sea bass	1	5.88				
Centropristis ocyurus						

untrawlable wrecks in the same area support dense thickets. The incidence of trawling is sufficiently high that the SAFMC requires local trawlers to use vessel monitoring systems. The council did not alter the penalties for trawling, however, which currently are relatively light (i.e., confiscated catch and moderate fines) and viewed by violators as a business expense (anonymous commercial fisherman, personal communication). This differs significantly in the Florida Keys National Marine Sanctuary, where, based on the National Marine Sanctuaries Act (U.S. Code, Title 16, chapter 32, section 1431 et seq., as amended in Public Law 106-513, November 2002), those guilty of destroying coral habitat—for whatever reason—are subject to fines substantial enough to cover the costs of habitat restoration or mitigation.

While surveillance and enforcement are important to management of MPAs, compliance indicates that extractive users perceive MPA boundaries as fair and equitable. This typically results from knowledge of the natural resources that occur within reserve boundaries and the ecological and economic benefits derived from their protection. Education clearly provides the most efficient, cost-effective, and powerful stimulus to habitat protection.

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