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Benthic Habitat Modification through Excavation by Red Grouper, *Epinephelus morio*, in the Northeastern Gulf of Mexico

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Abstract: Red grouper (*Epinephelus morio*) is an economically important species in the reef fish community of the southeastern United States, and especially the Gulf of Mexico. It is relatively common in karst regions of the Gulf and is associated with low-relief rocky features devoid of overlying sediments. Working both inshore in Florida Bay, Florida (U.S.A.), and offshore in the Gulf of Mexico shelf-edge fishery reserves, Madison Swanson and Steamboat Lumps, we characterized red-grouper habitat and the associated faunal assemblages and demonstrated through a series of experiments that red grouper expose rocky habitat by excavating with their mouths and fanning with their fins to clear away surficial sediment, thereby providing habitat for themselves as well as other reef-dwelling organisms. They also maintain this habitat by periodically clearing away sediment and debris. Such maintenance provides a clean rocky substrate for the attachment of sessile invertebrates, thereby modifying habitat features to provide refuge for many other species of fish and motile invertebrates. We demonstrated increased biodiversity and abundance associated with habitat structured by red grouper, and we speculate here as to its fishery importance as habitat for other economically important species such as spiny lobster (*Panulirus argus*) and vermilion snapper (*Rhomboplites aurorubens*).

INTRODUCTION

Architecturally complex habitats support species-rich assemblages [1–6]. The genesis of the architecture can be by physical processes, like wind, currents, or geological events, or in some cases the activities of resident organisms [7, 8]. Identifying these organisms and the effect of their habitat manipulations on diversity—as opposed to the more direct effects of predation [9, 10] or competition [6]—is an important and growing area of community interaction research.

Animals build structures for a variety of reasons that are largely related to competing needs for food, shelter, and procuring mates over the short term and for protecting young over the longer term. These “engineering” activities can have profound effects on local physical and biological habitat, thereby affecting other species at both local and landscape scales. This phenomenon is well known among terrestrial organisms ranging from beavers to prairie dogs [11, 12]. Beavers, for example, build dams to protect themselves and their broods from predation and weather and, in the process, alter the local hydrology and habitat heterogeneity for fishes, invertebrates, and migrating waterfowl [11] while increasing diversity of herbaceous plants over broader regions [13]. Prairie dogs, similarly, construct extensive burrow systems to serve as nurseries. These sites also provide refuge to a host of other species [12], affecting the diversity and abundance of a suite of predators, other burrowers, and avian communities [14].

Fewer studies have documented architectural activities in offshore marine systems, where observation and manipulation of organisms to establish cause and effect is more difficult. That said, a number of marine fish species do manipulate habitat. The better-known architects include eelpouts (Zoarcidae), gobies (Gobiidae), and tilefish (Malacanthidae). In the study reported here, we investigated such activities in red grouper.

The red grouper (*Epinephelus morio*, Serranidae) is a territorial, sedentary species that exhibits ontogenetically distinct habitat preferences, including a shallow-water-associated juvenile stage [15] and an offshore-reef-associated adult stage that is strongly associated with karst topography [16-19]. In particular, these fish favor limestone solution holes formed by past freshwater incursion. Normally, a solution hole acts as a sink, filling with sediments transported by bottom currents and surges until no longer visible from the surface. Where holes are exposed, they support a significantly more diverse community than the surrounding environment. Red grouper are strongly associated with exposed solution holes, to the extent that the holes are often called “grouper holes” [20, 21], but grouper have never been demonstrated to maintain these holes actively. If they do, the potential is

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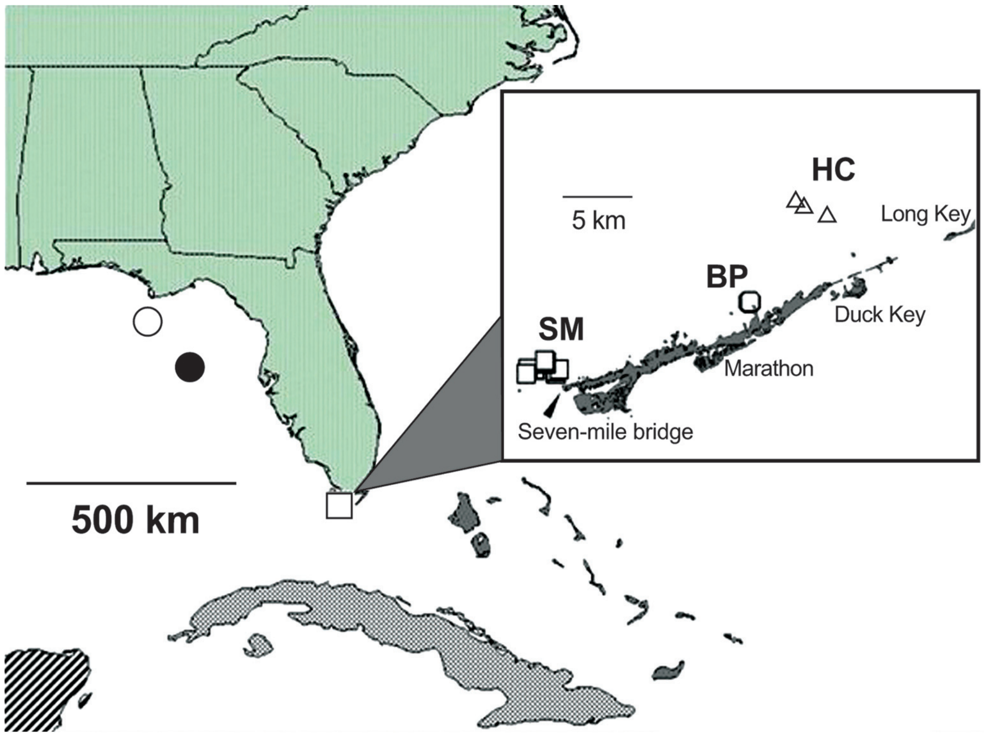

Fig. (1). Study sites in the northeastern Gulf of Mexico. Open circle, Madison Swanson Marine Reserve; black circle, Steamboat Lumps Marine Reserve; open square, Florida Keys (inset: HC, Hawks Cay; BP, Burnt Point; SM, Seven Mile Bridge).

great for community-level impacts. The objectives of our study were (1) to characterize the physical and faunal differences between red grouper holes and surrounding habitat and (2) to determine whether resident red grouper associated with these holes actively excavate and maintain the physical architecture within their habitat. Studies of the function of habitat manipulation based on findings from this study are currently under way.

METHODS

Our studies consisted of inshore and offshore components, representing, respectively, studies in juvenile and adult habitats. We evaluated juvenile habitat within Florida Bay in the Florida Keys (U.S.A.) in three areas—Hawk's Cay (HC) and Burnt Point (BP) (2000-2002) and Seven Mile Bridge (SM) (2002). We evaluated adult habitat offshore in the northeastern Gulf of Mexico within two marine reserves—the Steamboat Lumps Marine Reserve (SL) in 2000, 2001, 2004, and 2005 and the Madison Swanson Marine Reserve (MS) in 2004 (Fig. **1**; Table **1**). In juvenile habitat, we located grouper holes by towing scuba divers behind a boat at 1.0 kt in parallel transects over approximately 2.0 km^2 in each area. Divers temporarily marked suspected grouper holes with subsurface buoys and subsequently verified grouper presence at all sites. Using this method, we identified 24 sites each at HC and BP at water depths of 2 to 4 m and 28 grouper sites at SM at water depths of 3 to 7 m. We chose reference areas by drifting 50–100 m from each site and throwing a 1-m square quadrat from the boat. Because the direction of the current varied, this method provided a nonrandom but unbiased location for sites with which to compare habitat and diversity.

We located grouper holes offshore using a combination of fisher knowledge and side-scan sonar images; grouper presence was later verified during submarine and ROV surveys (described below). We entered all coordinates into a Global Positioning System database.

Verifying Habitat Manipulation by Red Grouper

In 2000, to determine whether juvenile red grouper could excavate solution holes in a limestone base at HC, we located sediment-filled solution holes by prodding the substrate with a 1-m fiberglass rod. Sites were chosen to have sediment depths of at least 0.3 m over a minimum area of 0.3 m^2 (roughly the size of a grouper-inhabited solution hole). We then placed an open-bottomed cage (1.0 m wide × 1.0 m long × 0.5 m high; mesh = 3 cm) over each of two such sites and placed a single juvenile red grouper (38–51 cm TL) in each cage. After 48 hours, we made visual observations of sediment movement patterns and evidence of digging activity.

In 2001, we investigated habitat maintenance at HC and BP by introducing 4 to 5 liters of aquarium-grade charcoal particles (high-purity activated charred-bone carbon, density > water; particle size 1.6–3.2 mm) into 13 naturally-occurring (= active) grouper holes (7 at HC, 6 at BP) at 0900 EST. Aquarium charcoal was used because it is nontoxic, easily distinguished from the naturally pale shell sand substrate surrounding the holes, and similar in particle size to existing substrate.

We checked sites for charcoal removal at 2-h intervals throughout the day. At all sites where charcoal removal occurred, we measured and recorded the maximum distance of deposition (using metric tape) and compass bearing from the

Table 1. Overview of Field Studies Related to Use of Habitat (Specifically Solution Holes in Hard Bottom) by Red Grouper (*Epinephelus morio*) During their Juvenile and Adult Life Stages Along the West Florida Shelf. BP, Burnt Point, Florida Bay; HC, Hawks Cay, Florida Bay. MS, SL, sites offshore on West Florida Shelf; RG, red grouper

Study Component	Hypothesis	Sites	Dates	Parameters Measured
Verification of habitat manipulation				
Caging experiment	RG excavate new holes when enclosed in cages	HC	2000	Presence of excavated hole, sediment movement
Charcoal removal from RG hole	Excavations maintained (i.e., hard substrate cleaned) by residents	HC, BP	2001	Pattern of charcoal distribution from hole; video observation of excavation behavior
RG removal from RG hole	RG holes retain charcoal when RG absent	HC, BP	2001	Charcoal distribution in/around hole; video observation of excavation behavior
Characterization of geology and benthic and fish assemblages around RG and references sites				
Juvenile habitat	RG holes house distinct/richer benthic and fish assemblages than reference areas.	BP, HC	2001	Sediment samples; photoquadrats of sites for benthic assemblage (% cover and species richness); video at different distances from holes for fish assemblages
Adult habitat	RG holes house distinct/richer diversity than reference areas.	MS, SL	2000, 2001 2004	Submersible, ROV video data; analysis of benthic habitat, species richness, abundance

grouper hole. In addition, we placed stationary video cameras at selected sites to record species' activity.

We also performed grouper removal experiments at each location. We identified six active grouper holes in each location. We removed grouper from three holes at each location and left the remaining three holes as controls (Table **2**). We introduced charcoal at all experimental and control sites immediately after grouper removal and then checked sites for charcoal removal after 24 h. Grouper were caught with circle hooks baited with squid and were transported in a live well approximately 15 km from the site, where they were held separately in moored cages until termination of the experiment. Fish were then tagged with individually numbered internal anchor tags and returned to their original sites.

Table 2. Experimental Design for Removal Studies of Red Grouper, *Epinephelus morio*, in the Florida Keys, U.S.A. Red Grouper were Left Undisturbed (R+) or Removed from Sites (R–). A Reference Site (C) for Comparison of Species Diversity and Abundance was Located Approximately 100 m South of Each Site

	Hawks Cay			Burnt Point		
No hole	CR–	CR–	CR–	CR–	CR–	CR–
No hole	CR+	CR+	CR+	CR+	CR+	CR+
Hole	R-	R-	R-	R-	R-	R-
Hole	R+	R+	R+	R+	R+	R+

Characterization of Habitat and Fish Assemblages (Juvenile)

At active red grouper holes at HC and BP in 2001 and 2002, we characterized habitat within temporary square quadrats (6 cell × 6 cell grid; cell size = 0.84 m^2) stabilized on sites with steel reinforcement-bar stakes. All sites were marked with underwater buoys so they could be relocated. We used unattached quadrats on grouper holes and reference sites at HC, BP, and SM in 2004. Although we did not characterize habitat at SM, it clearly differed from the HC and BP sites. The SM locations had strong tidal currents, in part because they were adjacent to a pass between two keys. The other two sites experienced weak currents. The HC locations were in an open area covered by sea grass and algal flats far from human-made structures, and BP locations were in areas with many rocky and coral outcrops near a seawall.

Sediment samples were collected from each site with a small shovel, and care was taken to retain fine-grained sediments. The textures of samples were classified according to the scheme of Shepard [22].

Quadrats were photographed with a digital still underwater camera (Olympus C3030 3.2 mega-pixel digital camera with a Tetra 30-30 underwater housing) for identification and quantification of biologically produced (*e.g.*, by coral, sessile invertebrates, and algae) and geologic cover at each site. We superimposed an array of 50 randomly distributed dots on each frame, identified the substrate immediately underneath each dot, and calculated percentage cover of each substrate type.

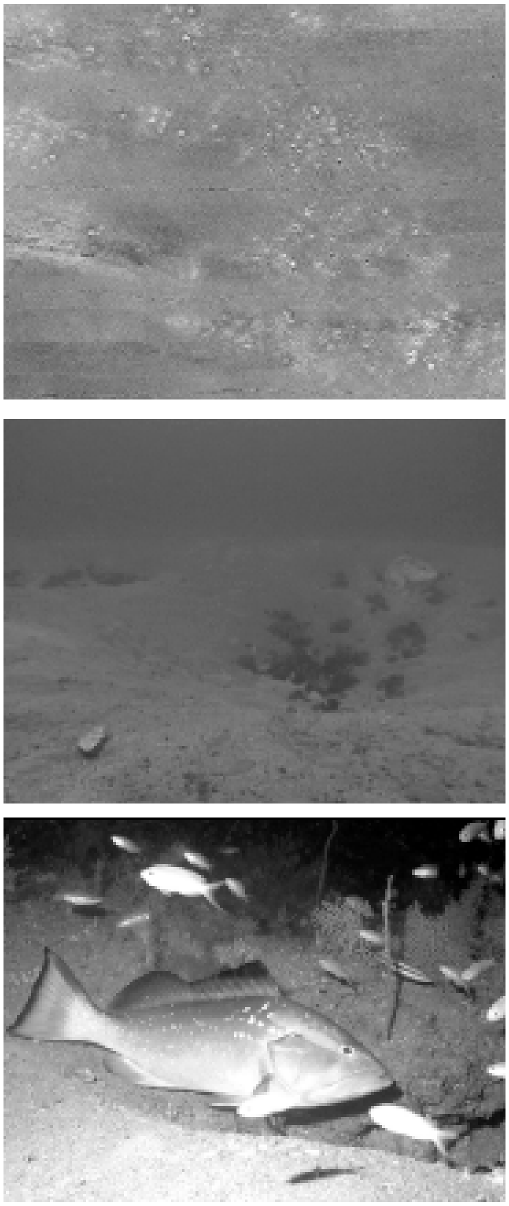

Fig. (2). Red grouper excavations in the northeastern Gulf of Mexico. Upper panel, side-scan sonar of the Steamboat Lumps Marine Reserve. Bright spots on the image are reflections from rocks at the center of each red grouper hole. Photo courtesy of the U. S. Geological Survey. Middle panel, a ground truth view of a red grouper hole with resident red grouper in attendance. Lower panel, edge of a grouper hole with red grouper in view.

We determined fish abundance, diversity, and habitat association at all sites. Divers conducted visual surveys to characterize the mobile fauna (to the lowest possible taxon) associated directly within and around all grouper holes in 2001. In 2002 we conducted stationary video-camera surveys by mounting three cameras along a randomly directed transect extending outward from the site. Camera views were perpendicular to the transect line at distances of 0 m, 3 m, and 6 m from the site; the view of the 0-m camera was directly across the solution hole. We turned on the cameras, left the site, and returned after 30 min to retrieve recordings. Video data included the minimum and maximum number of individuals and the activity pattern of each fish species observed at each station for each 30-min video segment. Activity patterns evaluated included milling (staying in the same spot or without directed motion for >5 sec) and traversing (actively moving across the station). We analyzed the differences in fish abundance among observations using linear regression. Abundance data were log transformed to normality. Because of the small number of sampled sites, we used the jackknife method to calculate species richness at 0, 3, and 6 m from the grouper holes.

Characterization of Habitat and Fish Assemblages (Adult)

We characterized geomorphology in the SL and MS in 2000 using side-scan sonar images (SIS 1000), chirp seismic-reflection profiles, and sediment samples collected by Van Veen grab [20] (Fig. **2**). Habitat and faunal assemblages were characterized by videography obtained by manned submersible (*DeepWorker,* Nuytco Research Inc., Vancouver British Columbia) in 2001 (50 h video) and by ROV (Deep Ocean Engineering Mini-Phantom) in 2004 and 2005 (20 h video) [20, 23].

For investigation of species density and abundance, each site was standardized as a circle of 4-m radius (= 50 m^2). In SL, we evaluated 18 active, 14 inactive, and 586 sand sites. In MS, we examined 12 active, 8 inactive, and 1019 sand sites. We used the Mann Whitney test to evaluate species diversity and abundance. For each site, we counted the numbers of individuals of each sessile benthic invertebrate species and determined the maximum and minimum counts for each fish species (maximum = total number seen on a given site). Although maximum counts typically overestimate the total number of individuals because of redundancy, minimum counts may be biased toward tightly schooling species. We then estimated species richness of active red grouper sites, viewing each site as a sample of a population of sites, using a jackknife method. We sampled haphazardly with the ROV and the submarine because of low visibility, variable currents, and limited time on the bottom.

RESULTS

Verification of Habitat Manipulation by Red Grouper

Each caged juvenile red grouper excavated sufficient sediment within 48 h to produce a subsurface excavation large enough to accommodate its entire body. Each fish actively moved sediment from solution holes to the inside perimeter of the cage (Fig. **3**). In one cage, the fish escaped by digging under the cage wall.

In the excavation maintenance experiments, charcoal removal (indicative of excavation maintenance) started within 2 h after charcoal was deposited at the sites (Fig. **4**). Most of the charcoal was removed and distributed around the site within 24 h. Red grouper removed charcoal with their mouths and deposited it on the sediment 1–3 m from the excavation. The direction of deposition varied, although it often occurred in the direction of the prevailing current.

Red grouper removal experiments revealed that the juvenile red grouper at these sites were the primary, and apparently only, species maintaining excavations. (Spiny lobster, a

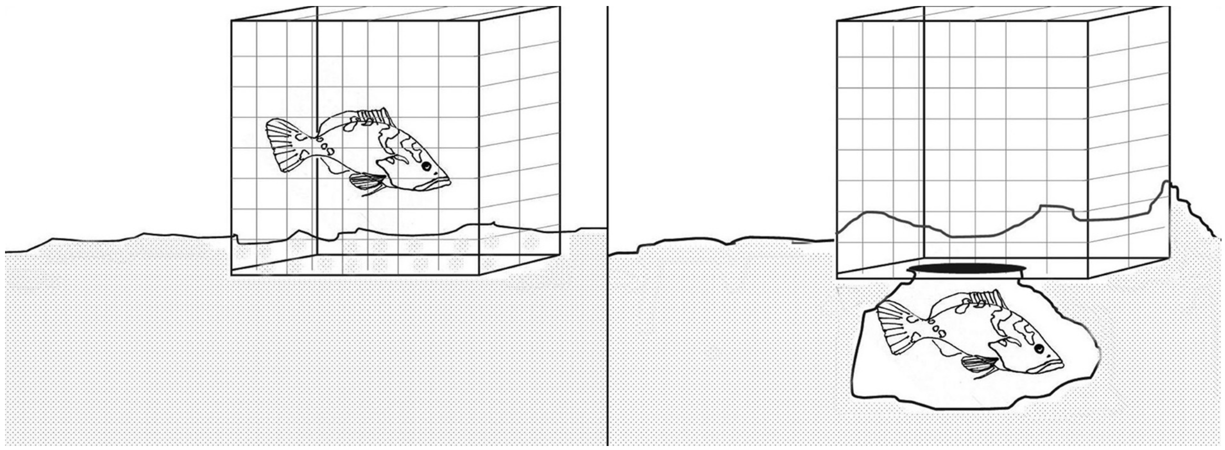

Fig. (3). Cartoon of caging experiment evaluating red grouper's ability to excavate.

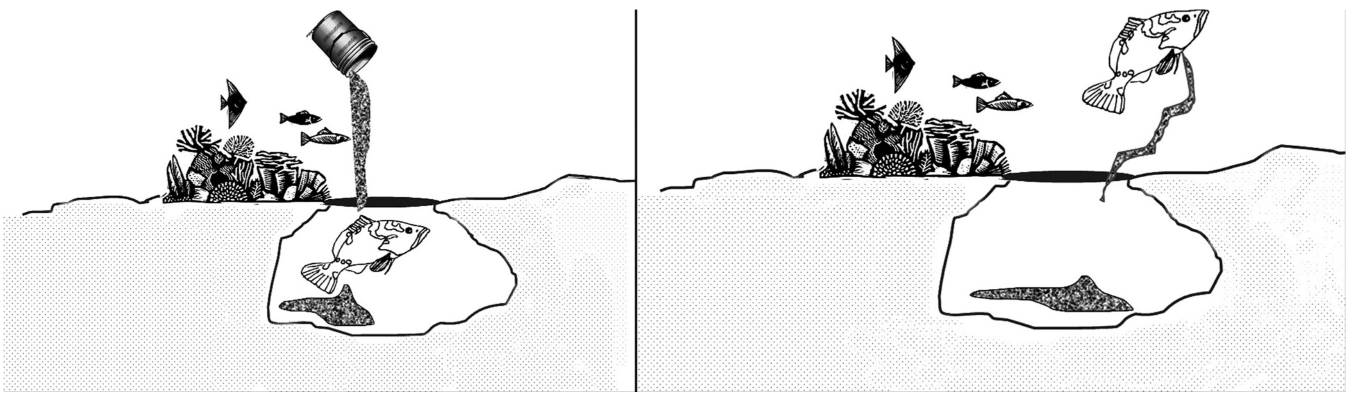

Fig. (4). Cartoon of charcoal distribution experiment in grouper hole.

common commensal in red grouper holes, pushed sediment around in only a very limited fashion.) Active distribution of charcoal occurred within 12 hours at sites harboring red grouper (n = 4), whereas no charcoal was distributed at sites from which grouper had been temporarily removed (n = 4).

Characterization of Habitat and Fish Assemblages (Juvenile)

Geomorphology of all solution holes in juvenile habitat was similar. All sediments contained at least 85% coarse particles (sand plus gravel) and could be classed as "sand" or "sand with gravel" (in which the gravel component was <50% or >10%). Particle composition was at least 95 % $CaC0_3$ primarily produced by coral, calcareous algae (*Halimeda* sp.*)*, and mollusks (Table **3**). Sediments produced a thin veneer over a perforated limestone base with numerous solution holes. Holes ranged in size from ~1.0 to 3.0 m^2 and depths up to 1 m.

The grouper holes and reference sites differed significantly in benthic cover (Fig. **5**). At HC and BP sites, the

Table 3. Sediment Composition from Solution Holes Occupied and maintained by Red Grouper, *Epinephelus morio*, in the Florida Keys, Collected in 2001. BP, Burnt Point; HC, Hawks Cay; Coarse, Sand Plus Gravel; Fine, Sand Plus Clay

Station	Sand	Gravel	Silt	Clay	Coarse	Fine	Total	Class
BP4b	80.09	13.24	4.46	2.2	93.33	6.66	99.99	Gravel >10%
BP14	84.34	8.2	5.39	2.07	92.54	7.46	100	Sand
BP16	74.19	12.02	9.45	4.34	86.21	13.79	100	Gravel >10%
HC18	89.1	2.94	4.51	3.45	92.04	7.96	100	Sand
BP6	74.13	10.94	10.37	4.56	85.07	14.93	100	Gravel >10%
BP6	86.75	8.69	2.75	1.82	95.44	4.57	100.01	Sand

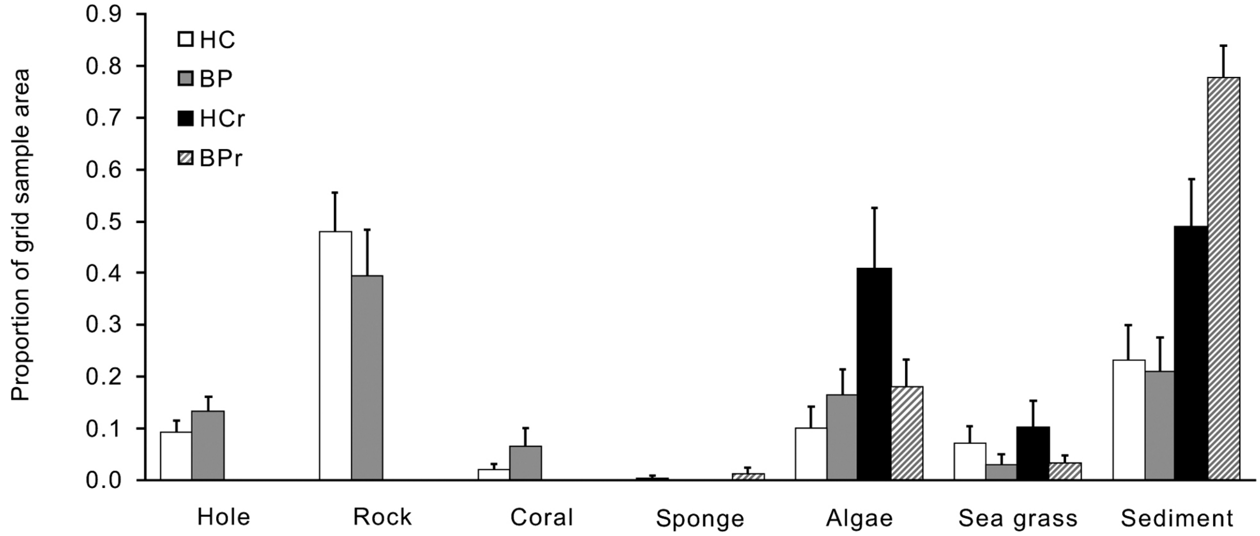

Fig. (5). Comparison of benthic cover at field sites in the Florida Keys sampled in 2001. HC, Hawk's Cay; BP, Burnt Point; r, reference site. "Hole" signifies an area actively maintained by resident grouper.

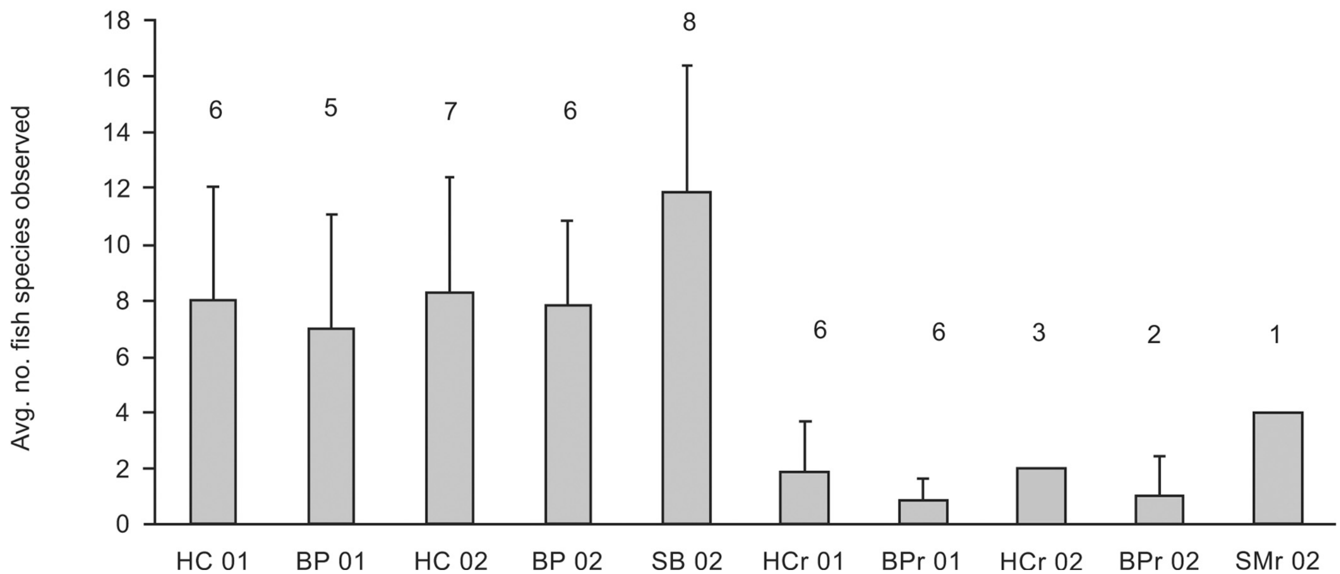

Fig. (6). Average number (and standard deviations) of fish species observed at grouper holes and references sites (r) in juvenile red grouper study areas in the Florida Keys, USA, in 2001 and 2002. Species counts were based on analysis of 30-min. video sampling by a remote camera at each site. Hawk's Cay (HC), and Burnt Point (BP) were sampled in 2001. Seven Mile Bridge (SM) was sampled in 2002 only. Numbers above bars represent number of sites.

primary substrate associated with grouper excavations was exposed rock with scleractinian corals, coralline algae, and anemones surrounded by sediment. Primary cover at reference sites was carbonate sediment, sea grass, and macroalgae.

We obtained data from 19 HC sites (7 at the hole, 5 from 3 m away, 7 from 6 m away), 16 BP sites (7 at the hole, 4 from 3 m away, 5 from 6 m away), and 28 SM sites (8 at the hole, 9 from 3 m away, 11 from 6 m away). The number of fish species associated with grouper holes (Tables **4**, **5**) was distributed normally according to a Shapiro-Wilk test ($P < 0.05$). The highest number of fish species occurred directly over holes occupied by red grouper (Fig. **6**; Table **5**). Cleaner fish—including juvenile blue angelfish and queen angelfish—occurred at active grouper sites, whereas none was found at reference sites. The cleaner shrimp, nestled among the tentacles of the excavation-associated anemone *Condolactis* sp., actively cleaned red grouper. The number of fish species

Table 4. List of Species Referred to in the Text and Tables

Common Name	Scientific Name
Almaco jack	*Seriola rivoliana*
Bandtail puffer	*Sphoeroides spengleri*
Bank butterflyfish	*Chaetodon aya*
Bank sea bass	*Centropristis ocyurus*
Blackbar drum	*Equetus iwamotoi*
Black grouper	*Mycteroperca bonaci*
Blue angelfish	*Holacanthus bermudensis*
Blue tang	*Acanthurus coeruleus*
Bluehead wrasse	*Thalassoma bifasciatum*
Blue runner	*Caranx crysos*
Bucktooth parrotfish	*Sparisoma radians*
Cleaner shrimp	*Periclimines pedersoni*
Cocoa damselfish	*Stegastes variabilis*
Cottonwick	*Haemulon melanurum*
Creole fish	*Paranthias furcifer*
Cubbyu	*Pareques umbrosus*
Damselfish	*Pomacentrus* sp.
Doctorfish	*Acanthurus chirurgus*
Emerald parrotfish	*Nicholsina usta*
Flamefish	*Apogon maculatus*
Foureye butterflyfish	*Chaetodon capistratus*
French angelfish	*Pomacanthus paru*
French grunt	*Haemulon flavolineatum*
Garden eel	*Heteroconger spp*
Goby sp.	Gobiidae
Grass porgy	*Calamus arctifrons*
Gray angelfish	*Pomacantus arcuatus*
Gray snapper	*Lutjanus griseus*
Gray triggerfish	*Balistes capriscus*
Greenband wrasse	*Halichoeres bathyphilus*
Grey triggerfish	*Balistes capriscus*
Grunt	*Haemulon* sp.
Highhat	*Pareques acuminatus*
Hogfish	*Lachnolaimus maximus*
Honeycomb cowfish	*Lactophrys polygonia*
Jackknife fish	*Equetus lanceolatus*
Lane snapper	*Lutjanus synagris*
Lizardfish	*Synodus foetens*
Ocean surgeon	*Acanthurus bahianus*
Ocellate skate	*Raja ackleyi*
Parrotfish	*Sparisoma* sp.
Pinfish	*Lagodon rhomboides*
Planehead filefish	*Stephanolepis hispidus*
Porgy	Sparidae
Porkfish	*Anisotremus viginicus*
Queen angelfish	*Holacanthus ciliarus*
Red barbier	*Hemanthias vivanus*
Red grouper	*Epinephelus morio*
Red porgy	*Pagrus pagrus*
Red snapper	*Lutjanus campechanus*
Red snapper	*Lutjanus campechanus*
Redband parrotfish	*Sparisoma aurofrenatum*
Reticulate moray	*Muraena retifera*
Roughtongue bass	*Holanthias martinicensis*
Sailors choice	*Haemulon parrai*
Sand perch	*Diplectrum formosum*
Saucereye porgy	*Calamus calamus*
Scad	*Decapturus* sp.
Scalloped hammerhead	*Sphryna lewini*
Scamp	*Mycteroperca phenax*
Scrawled cowfish	*Acanthostracion quadricornis*
Sheepshead porgy	*Calamus penna*
Short bigeye	*Pristigenys alta*
Slippery dick	*Halichoeres bivitattus*
Spanish grunt	*Haemulon macrostomum*
Speckled hind	*Epinephelus drummondhayi*
Spiny lobster	*Panulirus argus*
Spotfin butterflyfish	*Chaetodon ocellatus*
Spotfin hogfish	*Bodianus pulchellus*
Spotted goatfish	*Psuedupeneus maculatus*
Squirrelfish	*Holocentrus sp.*
Stingray	*Dasyatis sp*
Stoplight parrotfish	*Sparisoma viride*
Striped burrfish	*Chaetodipterus faber*
Striped parrotfish	*Scarus iseri*
Tattler	*Seranus phoebe*
Tobaccofish	*Serranus tabacarius*
Tomtate	*Haemulon aurolineatum*
Two spot cardinalfish	*Apogon pseudomaculatus*
Vermilion snapper	*Rhomboplites aurorubens*
White grunt	*Haemulon plumieri*
Wrasse	*Halichoeres* sp.
Wrasse bass	*Liopropoma eukrines*
Wrasse sp.	*Labridae*
Yellow stingray	*Urolophus jamaicensis*
Yellowtail reeffish	*Chromis enchrysura*
Yellowtail snapper	*Ocyurus chrysurus*

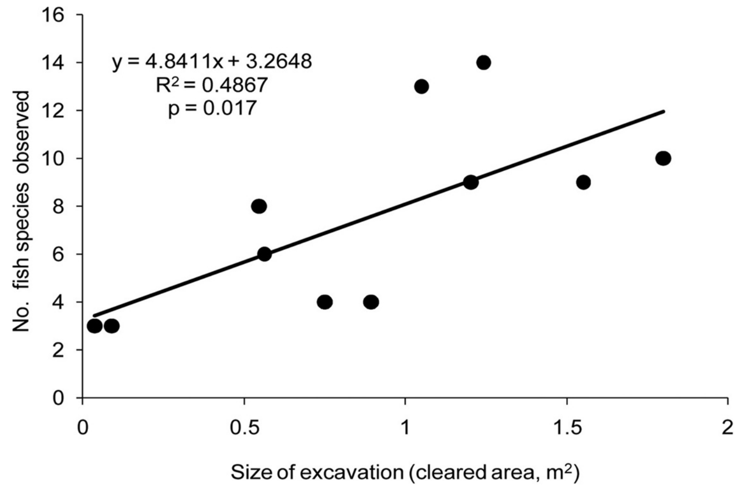

Fig. (7). Relationship between observed fish diversity and size of grouper hole for the combined Hawks Cay (HC) and Burnt Point (BP) sites in 2001. Species counts were based on analysis of 30-min. video sampling by a remote camera at each site. Area cleared of sediment at each site was estimated from diameter measurement at the site (by SCUBA divers).

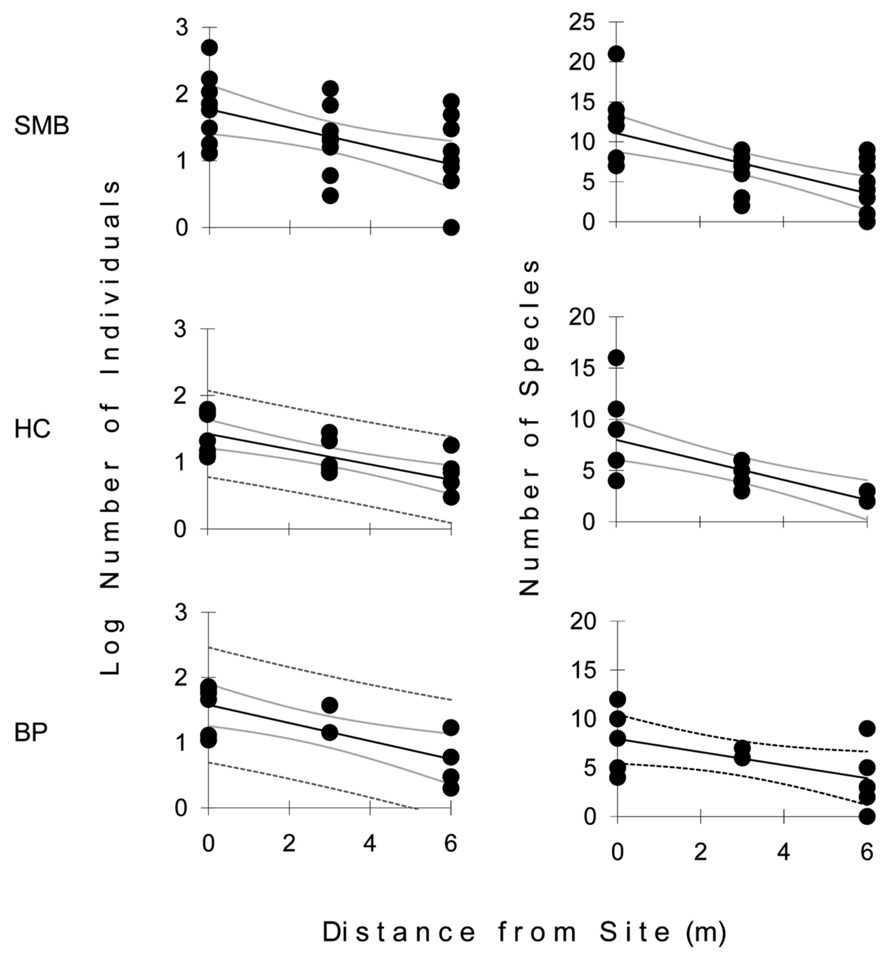

Fig. (8). Fish abundance and species diversity at three sites in the Florida Keys based on distance from red grouper *Epinephelus morio* holes. The average number of fish species at distant reference sites was between 1 and 4. $P < 0.05$ for all graphs. Black lines, predictions; gray lines, 95% confidence limits (CL). Fish abundance data were log transformed for normality. SM, Seven Mile Bridge; HC, Hawks Cay; BP, Burnt Point.

observed was positively correlated with the size of the excavated area (Fig. **7**).

Fish abundance and diversity both declined rapidly with distance from the hole (Fig. **8**). Milling behavior by fish associated with grouper holes was higher directly over the hole (= 0 m) than at distances of 3 m or 6 m, generally decreasing with distance from the excavation, suggesting that fish observed at the grouper site were residents of the immediate

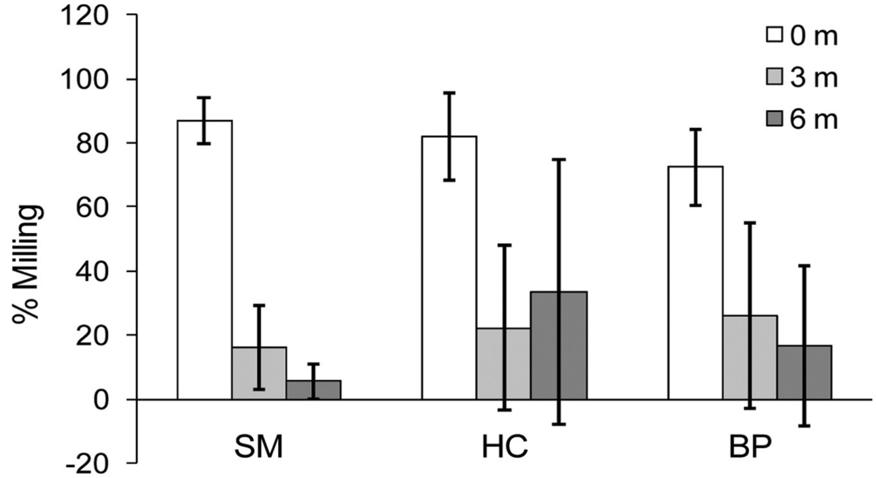

Fig. (9). Comparison of fish milling behavior at three areas in the Florida Keys, USA, as assessed by cameras located at 0, 3, and 6 m from grouper holes. SM, Seven Mile Bridge; HC, Hawk's Cay; BP, Burnt Point; Bars, 95 % CL.

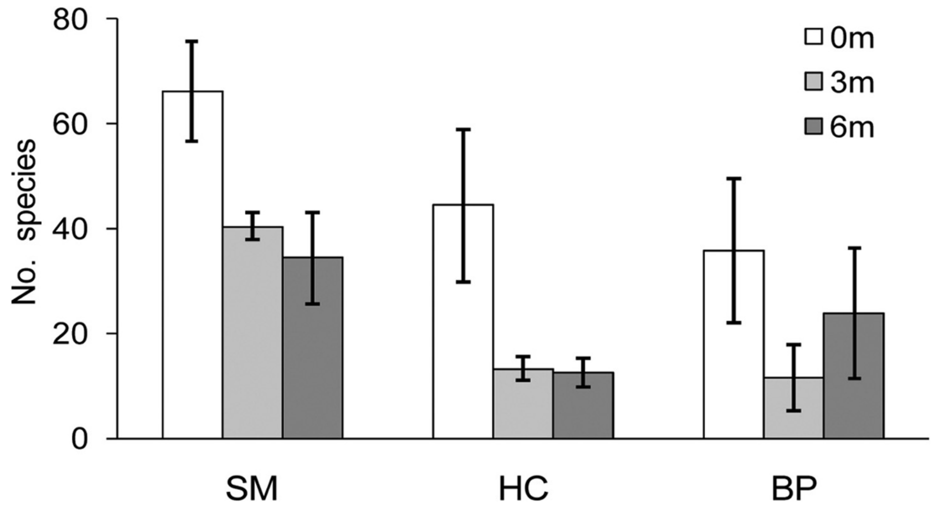

Fig. (10). Comparison of fish species richness at three areas in the Florida Keys, USA, as assessed by cameras located at 0, 3, and 6 m from grouper holes. SM, Seven Mile Bridge; HC, Hawk's Cay; BP, Burnt Point; Bars, 95 % CL.

area, whereas fish observed away from the site were in transit (Fig. **9**). We used a jackknife method to evaluate changes in species richness over distance (0m, 3m, and 6m) from red grouper holes at SM, HC, and BP. Fish species richness associated with grouper holes was highest at the 0 m site relative to sites 3 m or 6 m from the hole, generally decreasing with distance from the excavation (Fig. **10**).

Characterization of Habitat and Fish Assemblages (adult)

The SL red grouper habitat consisted of carbonate-rock hard bottom covered with a thick (up to 10 m) lens of carbonate-derived sediments. Embedded in these sediments were cone-shaped solution holes, each about 5 to 6 m in diameter (range <1 m to >25 m) and 1–2 m deep. Each hole had a cluster of carbonate-rock nodules at the bottom (mean diameter = 2.5 m; s.d. = 1.23, n = 3) covering roughly 36% of the area. Carbonate rocks were also embedded in the sloped sides of the large holes. Large holes were often surrounded peripherally by smaller satellite holes. Holes occurred in a clumped distribution at a density of about 250 km^{-2} [23].

The red grouper habitat in the MS was in the northeastern area and included significant low-relief (<1 m) carbonate-rock hard bottom in a large expanse of sand, differing from the SL in having a thin (<1 m) veneer of carbonate-derived sediments and in having far more relief.

Red grouper were more often present in sites that characterized by carbonate rock, either exposed at the centers of holes (SL) or on the surface (MS). We classified rock sites as active (= occupied by a resident red grouper) or inactive (= without a red grouper and filling with sediment).

Red grouper holes appeared to have distinct sessile species assemblages, depending on the availability of exposed rock substrate, although the quantification of assemblage structure was hampered by the poor resolution of sampling with remote platforms. Indeed, faunal richness for this community could not be determined because of poor lighting and the lack of a manipulator arm on the submersible for collecting samples. Most of the rock associated with SL holes was encrusted with sessile invertebrates (e.g., encrusting sponges, sea fans, corkscrew sea whips, and scattered clusters of *Oculina* coral) and crustose coralline algae; few benthic inverte-

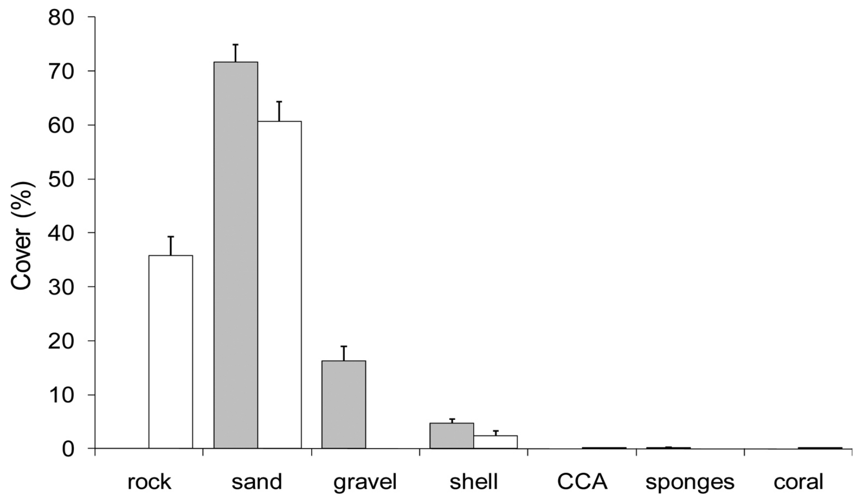

Fig. (11). Percentage cover of different substrate types in Steamboat Lumps Marine Reserve. White bars, grouper holes; grey bars, reference sites, CCA= crustose coralline algae.

brates occurred in the reference areas (except sponges, which were more abundant at reference sites) (Fig. **11**). Certain organisms were clearly associated only with grouper sites (e.g., sea urchins), whereas others occurred only in the sandy reference areas (e.g., arborescent bryozoans and a red fleshy alga).

Table 5. Relative Species Abundances at Three Grouper-Occupied Solution Holes Within Florida Bay, in 2001 or 2002.SM, Seven Mile Bridge; HC, Hawks Cay; BP, Burnt Point

Common Name	Relative Abundance		
	SM	HC	BP
Red grouper	5	6	3
White grunt	427	82	83
Sailors choice	151	0	5
Grunt	105	23	85
Tomtate	50	3	1
French grunt	30	1	0
Redband parrotfish	23	10	6
Lane snapper	21	4	5
Gray snapper	14	55	23
Yellowtail snapper	3	3	12
Hogfish	13	4	9
Wrasse	12	1	0
Bluehead wrasse	11	0	0
Doctorfish	11	3	1
Spotted goatfish	10	0	0
Gray angelfish	9	5	2
Gray triggerfish	6	2	0
Spiny lobster	6	3	10
Goby	5	0	0
Blue runner	4	2	0
Bucktooth parrotfish	4	0	0
Cottonwick	4	1	2
Spanish grunt	4	0	0
Black grouper	3	0	1
Porkfish	3	4	2
Sheepshead porgy	3	0	0

Common Name (cont.)	Relative Abundance		
	SM	HC	BP
Stoplight parrotfish	3	0	0
Blue tang	2	0	0
Cocoa damselfish	2	0	0
Cubbyu	2	0	0
Ocean surgeon	2	0	0
Slippery dick	2	0	2
Flamefish	1	0	0
Foureye butterflyfish	1	1	0
French angelfish	1	2	3
Grass porgy	1	1	0
Highhat	1	1	1
parrotfish	1	3	0
Pinfish	1	0	0
Porgy	1	1	0
Queen angelfish	1	0	0
Sand perch	1	1	0
Striped parrotfish	1	0	0
Tobaccofish	1	0	0
Yellow stingray	1	0	3
Bandtail puffer	0	1	0
Damselfish	0	1	4
Emerald parrotfish	0	1	0
Honeycomb cowfish	0	0	1
Planehead filefish	0	0	1
Saucereye porgy	0	7	0
Scalloped hammerhead	0	0	1
Scrawled cowfish	0	0	1

Table 6. Species Observed at Three Types of Habitat Sites in Steamboat Lumps Marine Reserve on the West Florida Shelf during 2001 or 2004. Active Sites, Sites at which a Resident Red Grouper Occupied a Solution Hole; Inactive Sites, Solution Holes Without Resident Red Grouper; Sand, Sites Without Obvious Architecture Complexity

	Active Sites		Inactive Sites		Sand
Common Name	**Mean no./50 m^2**	**%**	**Mean no./50 m^2**	**%**	**Mean no./50 m^2**
Red Grouper	1.00	100.00	0	0	0
Yellowtail reeffish	31.39	88.89	10.50	64.29	0.000
Red porgy	5.89	66.67	1.43	50.00	0.007
Vermilion snapper	21.83	61.11	6.57	42.86	0.007
Tomtate	30.11	50.00	1.50	7.14	0.002
Roughtongue bass	6.83	50.00	1.07	7.14	0
Bank sea bass	2.17	50.00	1.71	35.71	0.002
Bank butterflyfish	1.44	50.00	0.79	35.71	0
Tattler	0.83	50.00	0.86	42.86	0.007
Red barbier	5.11	38.89	3.57	14.29	0
Almaco jack	15.50	33.33	0.43	7.14	0
Creole fish	1.56	22.22	0.79	7.14	0
Red snapper	0.83	22.22	0.50	14.29	0
Jackknife fish	0.39	22.22	0.07	7.14	0
Wrasse sp.	0.56	16.67	0.43	14.29	0
Scamp	0.44	16.67	0	0	0.002
Scad	1.39	11.11	2.57	7.14	0
Squirrelfish	0.44	11.11	0.07	7.14	0
Green band wrasse	0.39	11.11	0	0	0
Two spot cardinalfish	0.22	11.11	0.21	7.14	0
Wrasse bass	0.17	11.11	0	0	0
Goby sp.	0.17	11.11	0.07	7.14	0
Short bigeye	0.83	5.56	0	0	0
Spotfin butterflyfish	0.22	5.56	0	0	0
Cubbyu	0.17	5.56	0	0	0
Slippery dick	0.11	5.56	0.29	7.14	0
Spotfin hogfish	0.06	5.56	0	0	0
Speckled hind	0.06	5.56	0	0	0
Grey triggerfish	0.06	5.56	0	0	0
Blue angelfish	0.06	5.56	0	0	0
Reticulate moray	0	0	0.07	7.14	0
Red snapper	0	0	0.07	7.14	0
Ocellate skate	0	0	0.07	7.14	0

Table 7. Species List for Three Types of Habitat Sites in Madison Swanson Marine Reserve on the West Florida Shelf Compiled for 2001 and 2004. (A) Active Sites are High-Relief Reef Sites Occupied by a Resident Red Grouper; (B) Inactive Sites Are High-Relief Reef Sites Without Resident Red Grouper; (C) Sand Sites have no Obvious Architectural Structure

	Active Sites		Inactive Sites		Sand
Common Name	Mean no./50 m^2	%	Mean no./50 m^2	%	Mean no./50 m^2
Red grouper	1.00	100.00	0	0	0
Roughtongue Bass	9.67	66.67	2.25	37.5	0
Yellowtail reeffish	7.83	58.33	8.75	50	0
Red porgy	1.25	58.33	0.13	12.5	0.004
Bank sea bass	2.42	58.33	1.38	37.5	0.001
Bank butterflyfish	1.33	58.33	1.25	50	0
Vermilion snapper	6.33	50.00	0	0	0
Short bigeye	0.50	41.67	0.38	25	0
Scamp	0.25	25.00	0.13	12.5	0
Cubbyu	2.42	25.00	0	0	0
Creole fish	0.92	25.00	0.38	12.5	0
Wrasse bass	0.42	16.67	0.13	12.5	0
Almaco jack	0.33	16.67	0	0	0
Tattler	0.08	8.33	0.13	12.5	0.004
Scad	8.33	8.33	0	0	0
Jacknife fish	0.25	8.33	0	0	0
Grey triggerfish	0.08	8.33	0	0	0
Blue angelfish	0.08	8.33	0.50	37.5	0
Blackbar drum	0.33	8.33	0	0	0
Two spot cardinalfish	0	0	0.13	12.5	0
Stingray	0	0	0	0	0.001
Striped burrfish	0	0	0.13	12.5	0
Spotfin butterflyfish	0	0	0.25	12.5	0
Lizardfish	0	0	0	0	0.001
Garden eel	0	0	0	0	0.001

The SL data revealed 33 fish species (Table **6**) and that for the MS 26 species (Table **7**). Because 2001 and 2004 did not differ in abundance or species data (Mann Whitney $P > 0.05$), we pooled data for these years. Active red grouper sites overall had greater species diversity and abundance than inactive sites or sand. SL and the MS active sites differed significantly in species diversity and abundance (Mann Whitney $P < 0.05$) and species richness (Jackknife method $P < 0.05$) (Fig. **12**). We found no association between hole diameter in the SL and either fish density or species abundance (Pearson's correlation coefficient $P > 0.05$).

We were able to videotape red grouper performing sediment maintenance at offshore sites at 76-m depths. The fish scooped up a mouthful of sediment (including shell hash) from the center of its excavation and swam about 10 m away before purging the sediment from its oral and opercular cavities. The fish allowed sediment initially to trail from the opercular chamber before actively ejecting it from the oral chamber and subsequently clearing it from both opercular chambers by strong opercular contractions. After completion of oral sediment transport, the fish returned to the excavation and swept the surface with its caudal fin, suspending a large cloud of sediment over the site.

DISCUSSION

We conclude from the results we report here that red grouper act as ecological engineers, actively excavating

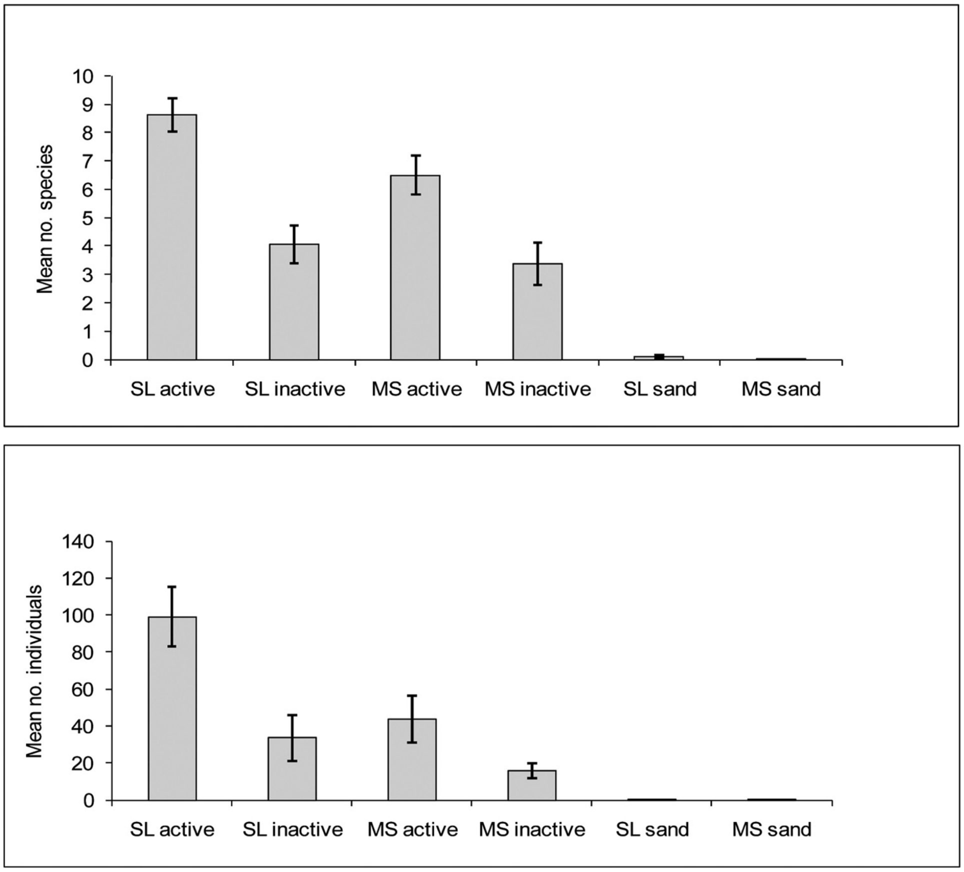

Fig. (12). Comparison of study sites on the West Florida Shelf within the Madison Swanson Marine Reserve (MS) and Steamboat Lumps Marine Reserve (SL). All sites were standardized to an area of 50 m^2. Upper panel, mean number of species; lower panel, mean number of individuals. Error bars indicate standard error. "Active" signifies a site with a red grouper present. "Inactive" signifies a site with no observed grouper activity.

sediment from and maintaining sediment-free habitat around solutions holes in hard bottoms in the northeastern Gulf of Mexico. Combining these results with data from newly settled juveniles reared in captivity, which began digging immediately after settlement (C. Koenig, unpublished data), we conclude that this behavior is maintained throughout the grouper's lifetime.

Red grouper exhibit strong site fidelity, remaining in the same hole for long periods. One of the juveniles we identified in the summer of 2000 retained residence in the same grouper hole for over a year. Three individuals acoustically tagged in July 2002 were relocated after four months, two at exactly the same site and another within 100 m of its original site. On the shelf edge, where two of us (Koenig and Coleman) are conducting tagging studies, 14 of 15 tag returns for adult red grouper indicated no movement from original tagging sites over a one-year period.

We also found that the sites with the greatest amount of architectural structure (e.g., greater spatial extent, number of entrances, and the presence of large encrusting corals) are preferred by red grouper. When a grouper was removed from a historically stable site (as opposed to a site that appeared to have been recently excavated), a new red grouper occupied the site within 24 h. Repeated removals were required before we could safely say that these sites were not occupied by resident red grouper. Similar results were not obtained at lower-relief sites.

Further, we suspect that these are multigenerational sites. Some actively maintained red grouper holes within Florida Bay harbored large heads (>0.3 m in diameter) of stony coral, sponges, and anemones that would suggest long-term maintenance of the site, certainly for periods longer than the residence time of the juvenile stage of an individual fish (4–5 years). Grouper holes in the deeper waters of the shelf break are so large (up to 5 m across and 2 m deep) that a substantial amount of time would be necessary for their complete excavation.

Our conclusion from both inshore and offshore studies is that active sediment removal by red grouper increases biological diversity by (1) exposing rocky substrate that provides settlement sites for sessile organisms and (2) increasing architectural complexity, which attracts many reef-associated species and provides shelter for juvenile stages of some economically important species. Red grouper holes are dramatically different from surrounding habitat and harbor a distinct community of hard-substrate-associated species, Although none of the species we observed is restricted to grouper holes, many are reef species that are not otherwise present in surrounding reference sites except as transients.

Potential benefits for these species include protection from roving predators, increased availability of prey, and perhaps, as occurs in tilefish burrows, close proximity to cleaning stations—all of which contribute to the biodiversity of the area.

The benefits of excavation to red grouper is another question. From their behavior, we are encouraged to pursue three distinct lines of inquiry: (1) the potential health benefits of attracting cleaner species; (2) the trophic benefit of attracting food; and (3) the reproductive benefits of attracting mates. We are presently engaged in studies of grouper reproductive behavior and have observed females entering the sites of males (and not the other way around) during the spawning season.

FISHERY IMPLICATIONS

We found several economically important species associated with red grouper holes. Inshore, we found black grouper and spiny lobster of harvestable size. The association with lobster is of considerable interest because of its high frequency. Lobsters are nocturnal predators, seeking refuge during the day. In much of the shallow hard-bottom region we studied, grouper holes provide important diurnal refugia for them. Because lobster survival is strongly correlated with shelter availability [24-26], the occurrence of grouper holes could influence lobster survivorship in a region where recreational lobster fishing is intense. (Nearly 50,000 recreational lobster fishers participate in a 2-day recreational season in late July, and nearly 60,000 participate in the first month alone of a later eight-month season.) Offshore, we found that red grouper holes attracted almaco jacks, red porgy, and significant numbers of juvenile vermilion snapper. The extent to which these sites serve as nursery habitat for vermilion is unknown, but we have not seen similar densities of vermilion anywhere else.

Red grouper have been harvested in the United States since the 1880s and are currently the most common grouper species landed in both commercial and recreational fisheries of the Gulf of Mexico. Juvenile red groupers are protected from exploitation to some extent by a size limit (currently 18 inches, 45.7 cm, for commercial fishing, http://www.gulfcouncil.org/Beta/GMFMCWeb/downloads/com%20brochure%202009-10.pdf, and 22 inches, 56 cm, for recreational fishing, http://www.gulfcouncil.org/Beta/GMFMCWeb/downloads/recbrochure2009-10.pdf, and 22 inches overall at the time of the study), but incidental catch and subsequent release of these fish may disrupt habitat maintenance. The extent to which juveniles are harvested during the intensive recreational lobster season is unknown, although we observed some harvest during the present study and suspect that the sheer number of people seeking lobsters in grouper holes certainly displaces them and may significantly increase movement away from their home sites.

Red grouper populations in the Gulf of Mexico and South Atlantic fishery regions of the southeastern United States have experienced intense fishing since the 1970s. They are clearly susceptible to exploitation [16]. The U. S. Atlantic coast population is overfished (http://www.nmfs.noaa.gov/sfa/domes_fish/StatusoFisheries/2008/4thQuarter/Summary_FSSI_Stocks.pdf), whereas the Gulf of Mexico population has alternately been considered overfished in the early 2000s and recovered a few years later [27, 28]. Its current status is being reevaluated (http://www.sefsc.noaa.gov/sedar/SEDAR_PlanSchedule_Jan2009.pdf), on the basis of concerns that red tide has had a substantial negative effect on recruitment that has influenced the population status (ftp://ftp.gulfcouncil.org/2009%20Gag%20and%20Red%20Grouper%20Update%20Assessment/). An update will be forthcoming within months.

Fishery removals, particularly those that exceed sustainable levels, can and often do have cascading effects in marine communities that ultimately result in the loss of biodiversity and extreme community flux [9, 10]. This situation arises when the captured species has a disproportionately large per capita influence on the system within which it lives. We contend that red grouper, through habitat manipulation, play an important role in increasing biodiversity and influencing community dynamics. Its loss through fishing could therefore erode local biodiversity. Indeed, the problem is perhaps exacerbated for species like red grouper and tilefish that have multiple ecological roles that may have synergistic influences on biodiversity over broad spatial scales.

Red grouper clearly remove sufficient carbonate sediment to transform an otherwise two-dimensional area into a three-dimensional structure below the seafloor, providing refuge for themselves and for other organisms. In the process, they expose hard substrate, thus creating settlement sites for corals, sponges, and anemones, allowing the creation of three-dimensional structure *above* the seafloor as well. Addition of these roles to their trophic contribution as resident apex predators suggests that they might have a disproportionately large per capita influence on the ecosystem within which they live. Demonstration of the interaction strengths between the engineer and the other species associated with the restructured habitat would reveal the system's level of dependence on the activities of the red grouper itself.

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REFERENCES

[1] Sale PF, Dybdahl R. Determinants in community structure for coral reef fishes in an experimental habitat. Ecology 1975; 56: 1343-45.

[2] Williams DM. In: Sale PF, Ed. The ecology of fishes on coral reefs. San Diego: Academic Press; 1991; pp. 437-74.

[3] Auster PJ, Malatesta RJ, LaRosa SC. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Mar Ecol Prog Ser 1995; 127: 77-85.

[4] Auster PJ, Joy K, Valentine PC. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). Environ Biol Fish 2001; 60: 331-46.

[5] Diaz RJ, Cutter GR, Able KW. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 2003; 26: 12-20.

[6] Fishelson L. Coral and fish biocoenosis: ecological cells gradually maturing in complexity, species composition and energy turnover. Environ Biol Fish 2003; 68: 391-405.

[7] Jones CG, Lawton JH, Shachak M. Organisms as ecosystem engineers. Oikos 1994; 69: 373-86.

[8] Jones CG, Lawton JH, Shachak M. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 1997; 78: 1946-57.

[9] Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. Fishing down the marine food webs. Science 1998; 279: 860-3.

[10] Steneck RS. Human influences on coastal ecosystems: does overfishing create trophic cascades? Trends Ecol Evol 1998; 13: 429-30.

[11] Gould JL, Gould CG. Animal architects: building and the evolution of intelligence. New York: Basic Books 2007.

[12] Hoogland JF. The black tailed prairie dog: social life of a burrowing animal. Chicago, Illinois: University of Chicago Press 1995.

[13] Wright JP, Jones CG, Flecker AS. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 2002; 132: 96-101.

[14] Smith GA, Lomolino MV. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia 2003; 138: 592-602.

[15] Moe MAJ. Biology of the red grouper (*Epinephelus morio* Valenciennes) from the eastern Gulf of Mexico. Professional Papers Series 10, Florida Marine Laboratory, St. Petersburg, FL. 1969; 95 p. 95.

[16] Coleman FC, Koenig CC, Collins LA. Reproductive styles of shallow-water grouper (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environ Biol Fish 1996; 47: 129-41.

[17] Koenig C, Coleman FC, Eklund AM, Schull J, Ueland JS. Mangroves as essential nursery habitat for goliath grouper (*Epinephelus itajara*). Bull Mar Sci 2007; 80: 567-86.

[18] Wilson RR, Burns KM. Potential survival of released groupers caught deeper than 40 m based on shipboard and *in-situ* observations, and tag-recapture data. Bull Mar Sci 1996; 58: 234-47.

[19]. Schirripa MJ, Legault CM, Ortiz M. The red grouper fishery of the Gulf of Mexico: Assessment 3.0. Stock assessment SFD 98-99-56, Sustainable Fisheries Division, Southeast Fisheries Science Center, Miami, Florida. 1999; p. 58.

[20] Scanlon KM, Koenig CC, Coleman FC, Miller M. Importance of geology to fisheries management: examples from the northeastern Gulf of Mexico. Am Fish Soc Symp 2003; 36: 95-9.

[21] Coleman FC, Williams SL. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol Evol 2002; 17: 40-4.

[22] Shepard FP. Nomenclature based on sand-silt-clay ratios. J Sediment Petrol 1954; 24: 151-8.

[23] Scanlon KM, Coleman FC, Koenig CC. In: Barnes PW, Thomas JP, Eds. Benthic habitats and the effects of fishing. Bethesda, Maryland. Am Fish Soc 2005; 301-12.

[24] Herrnkind WF, Butler MJ. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobster *Panulirus argus*. Mar Ecol Prog Ser 1986; 34: 23-30.

[25] Eggleston DB, Lipcius RN, Miller DL, Cobacetina L. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Mar Ecol Prog Ser 1990; 62: 79-88.

[26] Smith KN, Herrnkind WF. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille)—influence of size and shelter. J Exp Mar Biol Ecol 1992; 157: 3-18.

[27] SEDAR (Southeast Data Assessment and Review). Stock Assessment Report Gulf of Mexico Red Grouper SEDAR 12. Southeast Fisheries Science Center, Charleston, South Carolina 2006.

[28] Cass-Calay SL, Brown CA. Stock assessment of red grouper (*Epinephelus morio*) in the U.S. Gulf of Mexico. Sustainable Fisheries Division Contribution No. SFD-2007-003, NOAA Fisheries, Southeast Fisheries Science Center, Miami, Florida 2007; p. 63.

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