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PROTECTION OF FISH SPAWNING HABITAT FOR THE CONSERVATION OF WARM-TEMPERATE REEF-FISH FISHERIES OF SHELF-EDGE REEFS OF FLORIDA

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ABSTRACT

We mapped and briefly describe the surficial geology of selected examples of shelf-edge reefs (50–120 m deep) of the southeastern United States, which are apparently derived from ancient Pleistocene shorelines and are intermittently distributed throughout the region. These reefs are ecologically significant because they support a diverse array of fish and invertebrate species, and they are the only aggregation spawning sites of gag (*Mycteroperca microlepis*), scamp (*M. phenax*), and other economically important reef fish. Our studies on the east Florida shelf in the Experimental *Oculina* Research Reserve show that extensive damage to the habitat-structuring coral *Oculina varicosa* has occurred in the past, apparently from trawling and dredging activities of the 1970s and later. On damaged or destroyed *Oculina* habitat, reef-fish abundance and diversity are low, whereas on intact habitat, reef-fish diversity is relatively high compared to historical diversity on the same site. The abundance and biomass of the economically important reef fish was much higher in the past than it is now, and spawning aggregations of gag and scamp have been lost or greatly reduced in size. On the west Florida shelf, fishers have concentrated on shelf-edge habitats for over 100 yrs, but fishing intensity increased dramatically in the 1980s. Those reefs are characterized by low abundance of economically important species. The degree and extent of habitat damage there is unknown. We recommend marine fishery reserves to protect habitat and for use in experimentally examining the potential production of unfished communities.

Ecosystem-oriented and single-species-oriented fishery management are based on very different goals and considerations. Ecosystem management embraces preservation of biodiversity, maintenance of ecosystem structure and function, and broad-scale climatic considerations, whereas single-species management, in practice, is concerned with optimum exploitation of desirable species. Traditional management plans, in this case, involve social, economic, and biological aspects of fisheries but rarely consider the interspecific or physical processes that impinge upon them. A marked departure from this attitude was reflected in the passage of the Magnuson-Stevens Fishery Management and Conservation Act of 1996, which in effect linked the goals of sustainable fishery production and ecosystem preservation by making habitat a central issue in the management of fisheries. Because the act requires the protection and/or restoration of essential fish habitat, it links preservation of habitat with sustainable production of fishery resources and basically encourages the ecosystem approach to fishery management.

Habitat is fundamentally important to fishery production because its loss can profoundly affect productivity (Dayton et al., 1995). Benthic trawling and dredging may be especially damaging (Jones, 1992; Kaiser, 1998; Pilskalin et al., 1998; Watling and Norse, 1998), but other practices, such as removal of apex predators (Goeden, 1982) and other ecologically important species (McClanahan et al., 1999), may have equally severe repercussions. In fact, because marine benthic fisheries focus most intensely on apex predators (e.g., groupers, snappers, amberjacks, sharks), these species are commonly reduced or absent in heavily fished systems. The complete extent of ecosystem changes is unknown in most cases because virtually all areas have been fished for so many years that society has lost any historical perspective (Jackson, 1997). The condition of the habitat now considered 'normal' is probably far from the original baseline.

Reef-fish fisheries management of the southeastern United States is conducted primarily by the single-species approach, which ignores a number of germane facts: (1) that dozens of reef-fish species overlap in their distributions, (2) that they have complex interactions with each other and with the rest of their biotic and abiotic environment, and (3) that the fishery is extremely complex. As a result, regulation is complicated and data gathering requirements so demanding that the expense can exceed the value of the fishery itself.

Marine reserves (zones of nonconsumptive use) may provide both a means of circumventing these problems and a measure of insurance against the uncertainty and risk involved in our dependence on stock assessments and the conventional management process. For these safeguards to work, however, selection of marine reserve sites must be supported by at least some basic understanding of the life cycles and the habitat requirements associated with various developmental stages of the managed stocks.

In this paper we discuss the habitat and faunal characteristics of Florida's continental shelf edge (about 50 to 120 m), a region that is important ecologically as a source area for a diverse array of shelf and coastal marine species (Moe, 1963; Smith et al., 1975). Because some of these areas have experienced significant trawling and dredging efforts over the years, particularly off the east coast, mapping efforts are of considerable interest. In areas where habitat damage is significant, it is highly likely that the associated faunal communities are equally affected. Particularly at risk are economically important reef fish species, such as gag (*Mycteroperca microlepis*) and scamp (*M. phenax*), both protogynous species that are attracted to high-relief sites, where they aggregate to spawn and become vulnerable to exploitation (Gilmore and Jones, 1992; Coleman et al., 1996). Our objectives were to map the topographical, geological, and ecological features in defined areas on both the east and west coasts of Florida and to characterize the associated reef-fish communities, particularly where significant spawning habitat occurs. In doing so, we hope to provide baseline information for choosing appropriate reserve sites and for evaluating the effects of fully protected marine reserves on resident populations. We also briefly discuss the utility of marine reserves in habitat restoration projects.

STUDY SITES

High-relief shelf-edge reefs of the southeastern United States occur in a discrete depth zone (about 50 to 100 m) and appear, on the basis of their geomorphology, to have common Pleistocene origins (Ludwick and Walton, 1957; MacIntyre and Milliman, 1970; Avent et al., 1977; Parker et al., 1983; Sager et al., 1992; Benson et al., 1997). Our primary shelf-edge study site on the east coast of Florida occurs within the *Oculina* Banks, an area near the western edge of the Florida Current that extends from Fort Pierce to Cape Canaveral. The habitat consists of a series of clustered limestone pinnacles, 5 to 30 m in height, separated by a flat, soft-sediment bottom (Avent et al., 1977; Thompson et al., 1978; Thompson and Gilliland, 1980). The pinnacles are topped by the ivory tree coral, *Oculina varicosa*, which grows in spherical heads 1 to 2 m in diameter and provides the primary habitat structure of the reefs in this area (Reed, 1980). The South Atlantic Fishery Management Council in 1984 designated a 92-nmi^2 portion of this region a Habitat Area of Particular Concern (HAPC) to protect the coral from the damaging effects of mobile fishing gear, such as trawls and dredges. In 1994, the HAPC became the Experimental *Oculina* Research Reserve (EORR) when it was closed to all bottom fishing for a trial period of 10 yrs, primarily to protect grouper spawning aggregations (Fig. 1). In 1995, it was permanently closed to all anchoring. Trolling (fishing for pelagic fishes) is presently permitted within the EORR.

Shelf-edge reefs of the northeastern Gulf of Mexico extend along the 75-m isobath offshore of Panama City to just north of the Tortugas (Fig. 1; Schroeder et al., 1988, 1989). We have concentrated our efforts in the northeastern part of that range because it represents the dominant commercial fishing grounds for gag (Schirripa and Legault, 1997) and contains gag and scamp spawning aggregation sites (Coleman et al., 1996). These northeastern reefs include Madison Swanson (better known locally as Madison Swanson Rocks [locator charts, Sinbad Traders, P.O. Box 12282, Pensacola, Florida], but also referred to as Whoopie Grounds), Mud Banks (Ludwick and Walton, 1957; Moe, 1963), and Twin Ridges. Lower-relief shelf-edge reefs include The Edges and Steamboat Lumps. Other high-relief reefs off the western Florida Panhandle are associated with the rim of the Desoto Canyon (Ludwick and Walton, 1957; Continental Shelf Associates, 1992). Southern shelf-edge reef areas include Howell Hook, Pulley Ridge, Christmas Ridge, Hambone Ridge, and Northwest Peaks (Jordan and Stewart, 1959; Moe, 1963; Holmes, 1981; Continental Shelf Associates, 1992). The Gulf of Mexico Fishery Management Council (2000) has proposed Madison Swanson and Steamboat Lumps as new experimental no-take research reserves and is considering a proposal from the Florida Keys National Marine Sanctuary to extend the closure of Riley's Hump from a seasonal closure during spawning of mutton snapper (*Lutjanus analis*) to a year-round closure for all species.

Here, we describe our initial work on a 40-km segment of a shelf-edge reef, Twin Ridges, that lies northwest of the Florida Middle Grounds between the 60- and 75-m isobaths. This site was chosen from among other shelf-edge reefs because it is relatively small, is representative of west Florida shelf-edge reef habitat, and is currently fished.

METHODS

HABITAT DESCRIPTION.—We mapped east and west Florida shelf-edge habitat using side-scan sonar (tow speed, 3.5 to 4.0 knots) aboard the NOAA RV CHAPMAN. Ship navigation for the side-scan track lines was by Global Positioning System (GPS). Use of a military p-code descrambler increased accuracy to within 10–20 m. Digital mosaics of the side-scan images were made with the PCI Remote Sensing software package (Paskevich, 1996).

On the east Florida shelf, we mapped the EORR and a designated control (fished) area in 1995 (Fig. 1) with SIS-1000 side-scan sonar, with an ISIS digital data-logging system (yield, 375-m range; total swath width, 750 m; Malinverno et al., 1990; Danforth et al., 1991; Danforth, 1997). Track lines were spaced about 625 m apart, and overlap of the adjacent 375-m swaths was sufficient for digital mosaic construction. Resolution of the processed mosaics is about 2 m per pixel.

We collected sediment samples in regular patterns in the EORR at depths between 59 and 110 m using a van Veen grab sampler (n = 131). All sediment samples (except those composed of chunks of coral or coral rubble) were analyzed for particle size and carbonate content in the sedimentology laboratory of the U.S. Geological Survey at Woods Hole, Massachusetts. Texture terminology follows that of Folk (1974). The percent of calcium carbonate material was determined from weight loss of 15 g of bulk material after digestion with 10% HCl.

On the west Florida shelf in 1997, we mapped Twin Ridges, a 100-km^2 shelf-edge area (Fig. 1, site 6) using an EdgeTech DF1000 side-scan sonar system with an ISIS topside acquisition system (yield, 100-m range; total swath width, 200 m). Track lines were spaced at 150-m intervals; overlap

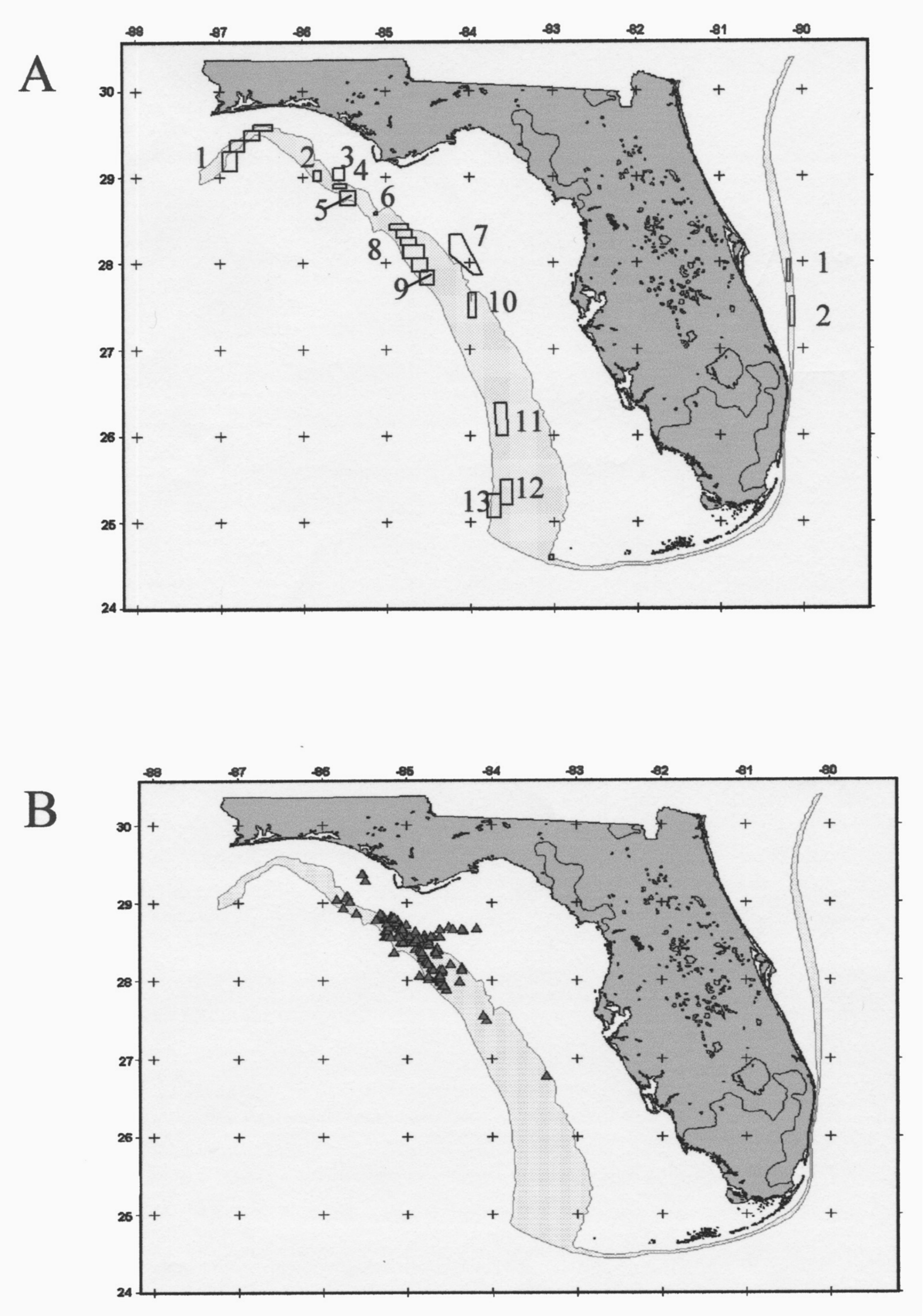

Figure 1. (A) Locations of potential and experimental shelf-edge marine reserve sites off Florida's coast. East coast: (1) Control (fished) site; (2) established Experimental *Oculina* Research Reserve. West coast: potential reserve sites: (1) 29 Edge/27 Edge (four blocks), (2) Woodward-Clyde Pinnacles, (3) 3-to-5s, (4) Mud Banks, (5) Madison Swanson, (6) Twin Ridges, (7) Florida Middle Grounds, (8) Edges (five blocks), (9) Steamboat Lumps, (10) Elbo, (11) Christmas Ridge, (12) Hambone Ridge, (13) Northwest Peaks, (14) Riley's Hump. (B) Locations of at-sea reef-fish catch locations on the west Florida shelf.

of the adjacent 200-m swaths was sufficient for digital mosaic construction. Resolution of the processed mosaics is about 1 m per pixel.

In addition to side-scan images, high-resolution seismic-reflection profile data were collected with a 300-joule Geopulse boomer. Penetrations of up to 0.07 s of two-way travel time (equivalent to several 10s of meters of sediment thickness, depending on the properties of the sediment) were achieved in some areas. About 1200 line-kilometers of echo-sounder data were also collected, with a 3.5-kHz system. Both sets of profile data were collected simultaneously with the side-scan sonar data and were recorded on a flatbed paper recorder. Water depth along the trackline was recorded digitally by the side-scan data acquisition system.

Sediment samples (n = 42) were collected with a van Veen sampler and analyzed in the same manner as those collected in the EORR.

Reef Fish Communities.—In the EORR we used a remotely operated vehicle (ROV), a fishery acoustic system (FAS), and manned submersible (Harbor Branch Oceanographic Institute's Clelia) videotape observations for describing habitat characteristics and reef-fish community composition and for observing grouper spawning aggregations. On west Florida shelf sites in 1997 and 1998, we used only ROV and FAS because the submersible was unavailable. All acoustic, ROV, submersible, and hook-and-line sampling was conducted during daylight hours (because most of the species of interest are diurnal) of late winter and early spring, the season that includes gag, scamp, and red grouper (*Epinephelus morio*) spawning.

We selected submersible dive sites on the basis of Gilmore and Jones's (1992) observations of grouper spawning aggregations, the presence of living *Oculina* habitat (Reed, 1980), and uniform representation of major topographical features in the reserve (Fig. 2). Dive transects consisted of nonlinear movements over and around the reefs. All data presented on fish abundance are from transect observations. We do not present data from FAS surveys because these data are currently incomplete. Videotapes were made during movement of the submersible (in some cases the camera scanned while the submersible was at rest). Submersible speeds were typically between 1 and 2 kt. Visibility varied from 3 to 6 m for all submersible dives. We were unable to dive at the control site because of poor weather conditions.

To evaluate temporal changes in the reef-fish communities, we compared videotapes taken at Jeff's Reef—a 4-ha double-pinnacle reef located at the southernmost end of the reserve—in the early spring of 1980 by R. G. Gilmore (Harbor Branch Oceanographic Institute) with those taken at the same site for this study (1995). We also examined within-year (1995) differences at five sites within the EORR, including Jeff's Reef, Chapman's Reef, Steeple, Twin Peaks, and Sebastian Pinnacles.

Videotapes were analyzed with a Sony Hi8 editing VCR (model EVO 9720) for reef-fish relative abundance. In all cases, fish counts were the maximum observed. Because we probably overestimated highly mobile pelagic species and underestimated cryptic species, we assumed that sampling bias was similar on all reefs because the same method of videotape sampling was used throughout.

Direct estimates of fish sizes were made during submersible dives from two laser points a known distance apart that were projected laterally onto the sides of the fishes as they were videotaped. Similar estimates could not be made for fish recorded in the 1980 videotapes because laser metric systems were unavailable at the time. We therefore made no corrections for apparent size differences between the 2 yrs, even though various morphological features of the fish indicated that individuals of economically important species were on average smaller in 1995 than in 1980. Biomass of economically important fishes was estimated by means of the length-weight relationship of gag ($Wt_{kg} = 8.15 \times 10^{-9}\ TL_{mm}^{\ 3.059}$), as reported by Bullock and Smith (1991). This relationship served as an approximation for all economically important species.

We used species richness and Morisita's index of similarity (Krebs, 1999) to compare reef-fish communities within the EORR and used rarefaction to standardize sample sizes for richness estimates. Morisita's similarity index was chosen because it is robust to differences in sample size and species diversity and varies from 0 (no similarity) to 1 (complete similarity). Because hook-and-line fishing in the region of the EORR has increased dramatically since 1980 (Gilmore, pers. comm.),

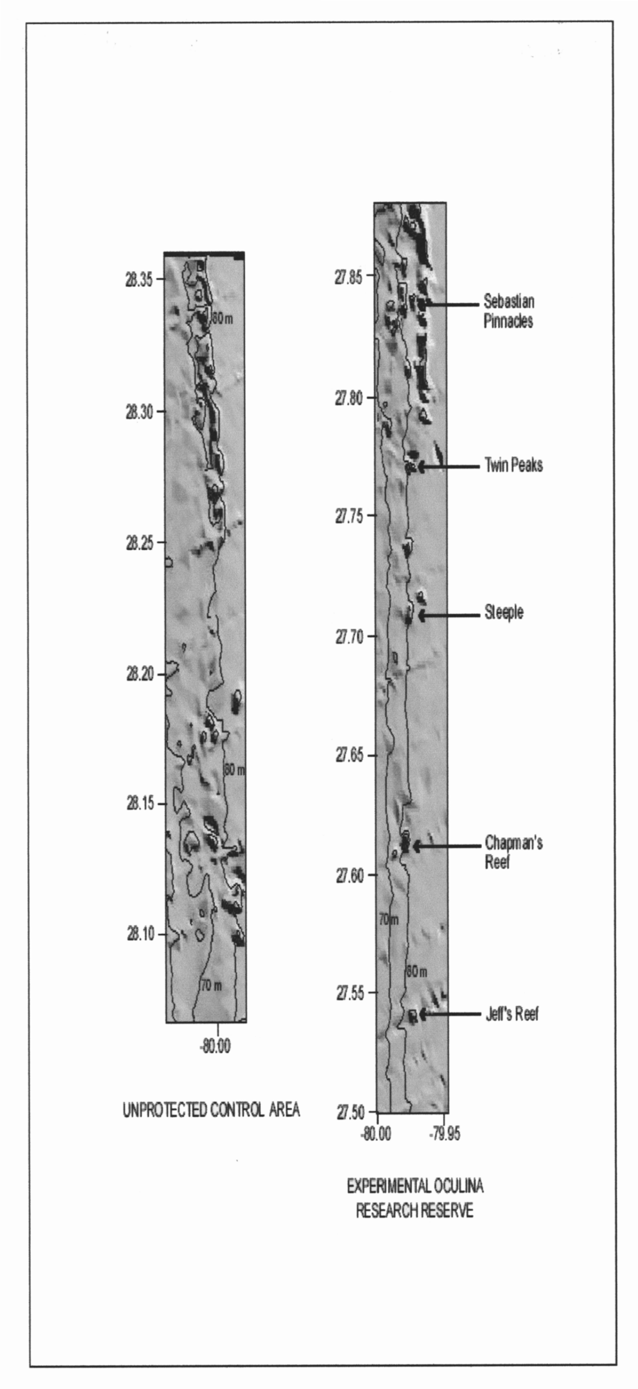

Figure 2. Shaded bathymetry map of the EORR and control sites on the east Florida shelf showing locations of sampling sites and pinnacle areas.

we compared numerical abundance and biomass of economically important fish species corrected for observation time. The rates, then, were the average number and average biomass of economically important species observed per minute of submersible observation time.

Fishing Patterns.—Information on reef-fish fishing patterns and on trawling and dredging activities around the EORR were obtained from interviews with fishers (Gilmore, pers. comm.) and published documents. Historical and present reef-fish fishing patterns on the west Florida shelf edge were derived from the literature (Camber, 1955; Moe, 1963; Schirripa and Legault, 1997), interviews with fishers, and at-sea sampling through the NMFS Panama City Laboratory.

We used a variety of information sources to identify significant historical and current fishery habitat in the eastern Gulf of Mexico. These included the Gulf of Mexico Fishery Management Council's (1998) Generic Amendment on Essential Fish Habitat, published accounts, interviews with commercial fishers, at-sea sampling aboard commercial and NOAA research vessels, and our personal knowledge of the life cycles of reef-fish species (Fig. 1). We identified grouper spawning sites on the basis of capture of reproductive individuals (females with hydrated eggs) and by videotape documentation of courtship behaviors (primarily in scamp).

Results

EORR and Control Sites

Habitat Descriptions.—We divided the *Oculina* Bank habitat into three general types based on the side-scan sonar data: high-relief/high-backscatter (HR/HB) areas, low-relief/high-backscatter (LR/HB) areas, and low-relief/low-backscatter (LR/LB) areas (Fig. 2). The HR/HB areas made up about 3% of the total area of the EORR. They appeared as multiple ridges and pinnacles concentrated along the 80-m isobath, rising above the surrounding seafloor to heights ranging from a few to 30 m. Two large, elongate areas of multiple peaks, ledges, and outcrops occur in the northern portions of both sites. The HR/HB terrain was typically rough and rocky and was the only terrain where *Oculina* thickets (or rubble) occurred. Sediment samples taken near the pinnacles and in scoured areas generally consisted of sand and gravel. Fine *Oculina* rubble was ubiquitous in these areas. Living *Oculina* was rare.

The LR/HB areas (70–90 m depths), generally surrounding the HR/HB areas, contained low (<1 m) relief rocky hard bottom. Much of the area was covered with gravelly carbonate sand. *Oculina* colonies, when present, were small. The remaining flat areas produced LR/LB acoustic returns and consisted of sands and muddy sands. Further details of the topography and geology are given by Scanlon et al. (1999).

We found that most of the *Oculina* habitat is severely degraded or destroyed, although the habitat at Jeff's Reef remained intact and essentially unchanged from 1980 to 1995. The coral structure on Chapman's Reef and the Steeple was heavily damaged, and that of Twin Peaks and Sebastian Pinnacles had been completely destroyed in all areas we surveyed. The habitat had been reduced to fine rubble of 2- to 3-cm pieces, as if repeatedly sieved. We cannot know the proportional area of *Oculina* habitat destruction without visualization of the bottom. Although no systematic coverage of the pinnacle area has been completed to date, we intend to use laser-line scan (Strand et al., 1997) for such mapping when funds permit.

Fish Communities.—The historical videotapes (1980) taken on submersible dives at Jeff's Reef (effort, 265 min transect time) showed a diverse assemblage of economically important species of the grouper-snapper complex (Table 1). Our 1995 videotapes from the same site (effort, 165 min transect time) showed distinct declines in mean abundance

Table 1. Percent composition of reef fish videotaped during submersible dives on Jeff's Reef in the EORR in the spring of 1980 (n = 4,375). Economically important species are marked with asterisks.

Species		Percentage
Scamp*	*Mycteroperca phenax*	35.724
Greater amberjack*	*Seriola dumerili*	30.174
Black sea bass*	*Centropristis striata*	5.002
Gag*	*Mycteroperca microlepis*	4.774
Red barbier	*Hemanthias vivanus*	4.568
Snowy grouper*	*Epinephelus niveatus*	4.089
Speckled hind*	*Epinephelus drummondhayi*	2.672
Red snapper*	*Lutjanus campechanus*	1.896
Roughtongue bass	*Holanthias martinicensis*	1.462
Red porgy*	*Pagrus pagrus*	0.937
Blue angelfish	*Holacanthus bermudensis*	0.731
Blackfin tuna*	*Thunnus atlanticus*	0.457
Bank butterflyfish	*Chaetodon aya*	0.297
Blackfin snapper*	*Lutjanus buccanella*	0.069
Gray snapper*	*Lutjanus griseus*	0.046
Cubbyu	*Equetus umbrosus*	0.046
Bank sea bass*	*Centropristis ocyurus*	0.046
Warsaw grouper*	*Epinephelus nigritus*	0.023
Porgy*	*Calamus* sp.	0.023
Reticulate moray	*Muraena retifera*	0.023
Soapfish	*Rypticus* sp.	0.023

and biomass (Fig. 3A,B) of these species. Most significantly, we found dramatic declines in gag and scamp spawning aggregations (compare Tables 1,2). The gag aggregation recorded by Gilmore and Jones (1992) was absent in 1995 and had not been reestablished on Jeff's Reef by 1999 (Koenig, unpubl. data). The two scamp aggregations, one on Jeff's Reef and one on Chapman's Reef, persisted over time but declined to a few small individuals at each site.

Reef-fish species diversity appeared to increase over time on Jeff's Reef, from 18 species (n = 4375; no. $\text{species}_{\text{actual}}$ = 22; no. $\text{species}_{\text{rarified}}$ = 18, SD = 1.35) to 38 species (n = 1399), although community similarity between the 2 yrs was low (Morisita's similarity index = 0.17).

Comparisons of the fish communities observed on Jeff's Reef in 1980 (Table 1) with those on Jeff's Reef in 1995 (Table 2) showed that dominance had shifted away from grouper species to small, nonfishery species, and that abundance had declined (Fig. 3). Within-year comparisons of intact (Table 2), degraded (Tables 3,4), and destroyed (Tables 5,6) habitat suggested that loss of habitat has a profound effect on diversity (Tables 2–6) and on the abundance and biomass of economically important fish species (Fig. 4). Twin Peaks and Sebastian Pinnacles (destroyed habitat) showed the lowest abundance of all the reefs. Expected and observed fish species diversity differed significantly on Chapman's Reef, Twin Peaks, and the Steeple but not on Sebastian Pinnacles (Table 7). Fish communities at Jeff's Reef, Chapman's Reef (effort, 37 min transect time) and Steeple (effort, 50 min transect time), where living *Oculina* habitat occurred, were similar to each other but

Table 2. Percent composition of reef fish videotaped during submersible dives on Jeff's Reef in the EORR in the spring of 1995 (n = 1,399). Economically important species are marked with asterisks.

Species		Percentage
Red barbier	*Hemanthias vivanus*	40.31
Roughtongue bass	*Holanthias martinicensis*	31.12
Vermilion snapper*	*Rhomboplites aurorubens*	7.00
Scamp*	*Mycteroperca phenax*	4.38
Yellowtail reeffish	*Chromis enchrysurus*	3.54
Tattler	*Serranus phoebe*	1.98
Blue angelfish	*Holacanthus bermudensis*	1.63
Grouper*	*Mycteroperca* sp.	0.99
Bank butterflyfish	*Chaetodon aya*	0.85
Reef butterflyfish	*Chaetodon sedentarius*	0.85
Short bigeye	*Pristigenys alta*	0.85
Tomtate	*Haemulon aurolineatum*	0.57
Wrasse bass	*Liopropoma eukrines*	0.57
Greater amberjack*	*Seriola dumerili*	0.57
Dwarf goatfish	*Upeneus parvus*	0.57
Porgy*	*Calamus* sp.	0.50
Bank sea bass*	*Centropristis ocyurus*	0.50
Red snapper*	*Lutjanus campechanus*	0.50
Lizardfish	*Synodus* sp.	0.50
Speckled hind*	*Epinephelus drummondhayi*	0.28
Spotfin butterflyfish	*Chaetodon ocellatus*	0.21
Bigeye	*Priacanthus arenatus*	0.21
Doctorfish	*Acanthurus chirurgus*	0.14
Butterflyfish	*Chaetodon* sp.	0.14
Damselfish	*Chromis* sp.	0.14
Flounder*	*Paralichthys* sp.	0.14
Whitespotted soapfish	*Rypticus maculatus*	0.14
Almaco jack*	*Seriola rivoliana*	0.14
Blue chromis	*Chromis cyanea*	0.07
Sand perch	*Diplectrum formosum*	0.07
Jackknife-fish	*Equetus lanceolatus*	0.07
Cubbyu	*Equetus umbrosus*	0.07
Squirrelfish	*Holocentrus* sp.	0.07
Gag*	*Mycteroperca microlepis*	0.07
Batfish	*Ogcocephalus* sp.	0.07
Scorpionfish	*Pontinus* sp.	0.07
Belted sandfish	*Serranus subligarius*	0.07
Puffer	*Sphoeroides* sp.	0.07

differed from those of the destroyed sites, Twin Peaks (effort, 42 min transect time) and Sebastian Pinnacles (effort, 29 min transect time; Table 8).

Fishing Patterns.—Three different fisheries have operated in the area of the *Oculina* Banks, including parts of the EORR, in the past 30 yrs: a trawl fishery for rock shrimp (*Sicyonia brevirostris*), a trawl and dredge fishery for calico scallops (*Argopecten gibbus*), and a hook-and-line fishery for reef fish. Both the rock shrimp and calico scallop

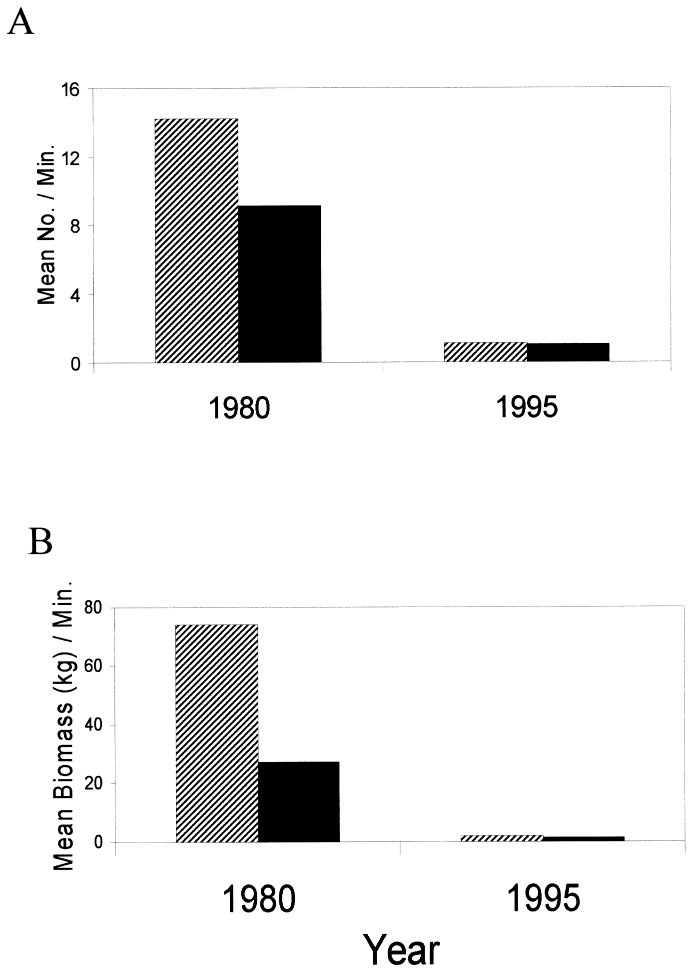

Figure 3. Comparison of historical (1980) and current (1995) populations of economically important fish species observed on submersible dives on Jeff's Reef within the EORR. (A) Abundance (mean number per minute videotape time); (B) biomass (mean biomass in kilograms per minute videotape time). Diagonal bars = pelagic species included; black bars = pelagic species excluded.

fisheries started in the early 1970s (Allen and Costello, 1972; Kennedy et al., 1977; Oleson, 1982). The rock shrimp fishery persists today, and although trawling in the EORR has been illegal since 1984, it is known to have occurred in the area as late as 1994. The scallop fishery collapsed in the late 1980s (Stimpson, 1989). Reef-fish fishing in this region increased in the early 1980s, especially on Jeff's Reef. Bottom fishing in the EORR has been illegal since 1994 but continued on Jeff's Reef and elsewhere in the EORR as late as 1997 (Koenig et al., 1997; Koenig, pers. observ.).

West Florida Shelf Edge

Habitat Descriptions.—In the area we surveyed on the west Florida shelf (60–75 m depth), we found two 6-km–long pronounced rocky ridges extending up to 15 m off the seabed (Fig. 5). The ridges, which we have called Twin Ridges, trend northwest, roughly

Table 3. Percent composition of reef fish videotaped during submersible dives on Chapman's Reef in the EORR in the spring of 1995 (n = 366). Economically important species are marked with asterisks.

Species		Percentage
Red barbier	*Hemanthias vivanus*	27.32
Roughtongue bass	*Holanthias martinicensis*	27.32
Red snapper*	*Lutjanus campechanus*	14.48
Dwarf goatfish	*Upeneus parvus*	8.20
Greater amberjack*	*Seriola dumerili*	6.01
Yellowtail reeffish	*Chromis enchrysurus*	5.74
Bank butterflyfish	*Chaetodon aya*	2.73
Scamp*	*Mycteroperca phenax*	2.19
Almaco jack*	*Seriola rivoliana*	1.37
Wrasse bass	*Liopropoma eukrines*	1.09
Reticulate moray	*Muraena retifera*	1.09
Blue angelfish	*Holacanthus bermudensis*	0.55
Porgy*	*Calamus* sp.	0.27
Leopard toadfish	*Opsanus pardus*	0.27
Cardinal soldierfish	*Plectrypops retrospinus*	0.27
Bluefish	*Pomatomus saltatrix*	0.27
Vermilion snapper*	*Rhomboplites aurorubens*	0.27
Whitespotted soapfish	*Rypticus maculatus*	0.27
Tattler	*Serranus phoebe*	0.27

Table 4. Percent composition of reef fish videotaped during submersible dives on the Steeple site of the EORR in the spring of 1995 (n = 180). Economically important species are marked with asterisks.

Species		Percentage
Roughtongue bass	*Holanthias martinicensis*	26.17
Red barbier	*Hemanthias vivanus*	25.91
Bank butterflyfish	*Chaetodon aya*	9.33
Purple reeffish	*Chromis scotti*	8.81
Scamp*	*Mycteroperca phenax*	7.77
Blue angelfish	*Holacanthus bermudensis*	4.40
Tattler	*Serranus phoebe*	3.63
Cardinal soldierfish	*Plectrypops retrospinus*	3.37
Reef butterflyfish	*Chaetodon sedentarius*	3.11
Short bigeye	*Pristigenys alta*	1.81
Creole fish	*Paranthias furcifer*	1.30
Speckled hind*	*Epinephelus drummondhayi*	0.78
Soapfish	*Rypticus* sp.	0.78
Red grouper*	*Epinephelus morio*	0.52
Wrasse bass	*Liopropoma eukrines*	0.52
Snapper*	*Lutjanus* sp.	0.52
Porgy*	*Calamus* sp.	0.26
Yellowtail reeffish	*Chromis enchrysurus*	0.26
Porcupinefish	*Diodon hystrix*	0.26
Moray	*Muraena* sp.	0.26
Scorpionfish	*Scorpaena* sp.	0.26

Table 5. Percent composition of reef fish videotaped during submersible dives on Twin Peaks in the EORR in the spring of 1995 (n = 194). Economically important species are marked with asterisks.

Species		Percentage
Greater amberjack*	*Seriola dumerili*	40.00
Almaco jack*	*Seriola rivoliana*	21.03
Cubbyu	*Equetus umbrosus*	12.82
Yellowtail reeffish	*Chromis enchrysurus*	6.67
Tattler	*Serranus phoebe*	5.64
Scamp*	*Mycteroperca phenax*	3.08
Bank butterflyfish	*Chaetodon aya*	2.56
Reef butterflyfish	*Chaetodon sedentarius*	2.56
Red snapper*	*Lutjanus campechanus*	2.05
Reticulate moray	*Muraena retifera*	1.54
Spotfin butterflyfish	*Chaetodon ocellatus*	1.03
Purple reeffish	*Chromis scotti*	0.51
Bluefish	*Pomatomus saltatrix*	0.51

Table 6. Percent composition of reef fish videotaped during submersible dives on Sebastian Pinnacles in the EORR in the spring of 1995 (n = 136). Economically important species are marked with asterisks.

Species		Percentage
Roughtongue bass	*Holanthias martinicensis*	36.76
Bank butterflyfish	*Chaetodon aya*	15.44
Tuna*	*Euthynnus* sp.	7.35
Scamp*	*Mycteroperca phenax*	5.88
Reef butterflyfish	*Chaetodon sedentarius*	5.15
Yellowtail reeffish	*Chromis enchrysurus*	5.15
Short bigeye	*Pristigenys alta*	5.15
Wrasse bass	*Liopropoma eukrines*	4.41
Tattler	*Serranus phoebe*	3.68
Blue angelfish	*Holacanthus bermudensis*	2.94
Almaco jack*	*Seriola rivoliana*	2.21
Red snapper*	*Lutjanus campechanus*	1.47
Bigeye	*Priacanthus arenatus*	1.47
Gag*	*Mycteroperca microlepis*	0.74
Leopard toadfish	*Opsanus pardus*	0.74
Scorpionfish	*Scorpaena* sp.	0.74
Greater amberjack*	*Seriola dumerili*	0.74

parallel to the present coastline of western Florida. Much of the area surrounding these limestone ridges is composed of sand and devoid of reef structure, but to the southeast and surrounding the ridges, we found large areas of low-relief hard bottom, as evidenced by strong returns from echo-sounder and seismic-reflection profiles. Side-scan images of the hard-bottom areas showed high backscatter with a high degree of subtle (compared to the high-relief outcrops) variability over short distances. These hard-bottom areas may have been overlain either partially or completely by a veneer of sediment. The side-scan mosaics, sediment analyses, and geologic interpretation are given by Scanlon et al. (in press).

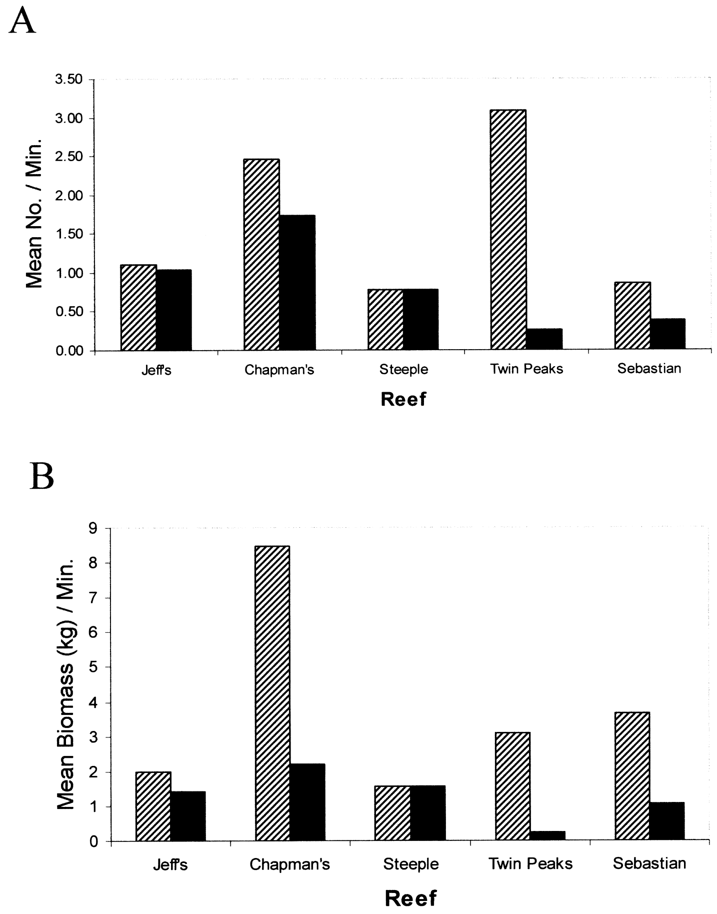

Figure 4. Comparison of populations of economically important fish species observed on submersible dives among 5 sampling sites within the EORR in 1995. (A) Abundance (mean number per minute videotape time); (B) biomass (mean biomass in kilograms per minute videotape time). Diagonal bars = pelagic species included; black bars = pelagic species excluded.

Fish Communities.—The reef fish community of Twin Ridges observed in 1997 and 1998 generally lacked large, economically important species (Table 9). This pattern persisted over all shelf-edge reefs we have surveyed since 1994 (Koenig, unpubl. data). Acoustic sampling of Twin Ridges showed high concentrations of small (indicated by high backscatter) and large fish (indicated by high target strength) associated with the rocky ridges, as expected. The largest fish observed with the ROV were scamp, so it is assumed that these fish produce the high-target-strength returns.

Fishing Patterns.—Commercial hook-and-line and longline fishers heavily fish the reef area we surveyed in this study. Although they have fished the shelf-edge reefs of west Florida in general since the late 1800s (Camber, 1955), pressure increased significantly in the early 1980s, when technological advances in navigation and positioning equipment allowed commercial longline and hook-and-line fishers to locate and concentrate on shelf-edge reefs and associated spawning aggregations of species such as gag and scamp

Table 7. Rarefaction of fish species richness at sites observed within the EORR in 1995.

Location	Habitat status	Number of individuals	Observed no. species	Expected no. species	SD
Jeff's Reef	Intact	1,399	38	–	–
Chapman's Reef	Damaged	380	19	25	2.2
The Steeple	Damaged	366	19	25	2.2
Twin Peaks	Destroyed	194	13	20	2.3
Sebastian Pinnacles	Destroyed	136	17	17	2.2

Table 8. Morisita's similarity matrix for fish communities at sites observed within the EORR in 1995. [1]Intact habitat, [2]damaged habitat, [3]destroyed habitat.

	Jeff's Reef[1]	Chapman's Reef[2]	The Steeple[2]	Twin Peaks[3]	Sebastian Pinnacles[3]
Jeff's Reef[1]	1.00	0.90	0.92	0.04	0.61
Chapman's Reef[2]	0.90	1.00	0.85	0.17	0.63
The Steeple[2]	0.92	0.85	1.00	0.04	0.72
Twin Peaks[3]	0.04	0.17	0.04	1.00	0.10
Sebastian Pinnacles[3]	0.61	0.63	0.72	0.10	1.00

(Schirripa and Legault, 1997). Because shelf-edge reefs of west Florida are far offshore, recreational fishermen rarely fish them.

We determined recent patterns of commercial reef-fish fishing from 11 sampling trips by NMFS Panama City Laboratory personnel aboard commercial hook-and-line vessels between 1991 and 1997 (Fig. 1B). Year-round, the majority of fishing occurred on shelf-edge reefs, and gag comprised about one-third of the catch overall (Table 10). Even those commercial fishers who typically fish elsewhere concentrate on gag during their aggregation period on shelf-edge reefs (Koenig et al., 1996; Schirripa and Legault, 1997).

Discussion

Habitat and the Effects of Fishing: Florida Shelf-edge Reefs

Northeast Florida.—Our studies in the EORR demonstrate that highly productive habitat has been and may continue to be destroyed by harmful fishing practices. The cumulative effects of spawning habitat destruction on fishery production are likely to be serious and synergistic with those produced by overfishing. Spatially heterogeneous areas offer far greater opportunities for resource partitioning among different species, resulting in higher species diversity than is found in more homogeneous habitats, such as fine coral rubble. Modification of the integrity of structure typically results in both a decrease in biomass and a loss of diversity. The reef-associated macroinvertebrate community inhabiting the interstices of intact, live, branching *Oculina* colonies nearly 20 yrs ago, for example, included as many as 100 species of molluscs and more than 200 species of crustaceans (Reed, 1980; Reed et al., 1982; Reed and Mikkelsen, 1987). None of these species has been found in denuded areas such as Sebastian Pinnacles.

We deduce that the *Oculina* habitat damage results from mechanical degradation such as trawling and dredging, because the nonliving bases of the coral heads are missing (or pulverized) from the areas of greatest damage. If coral heads had been removed by either

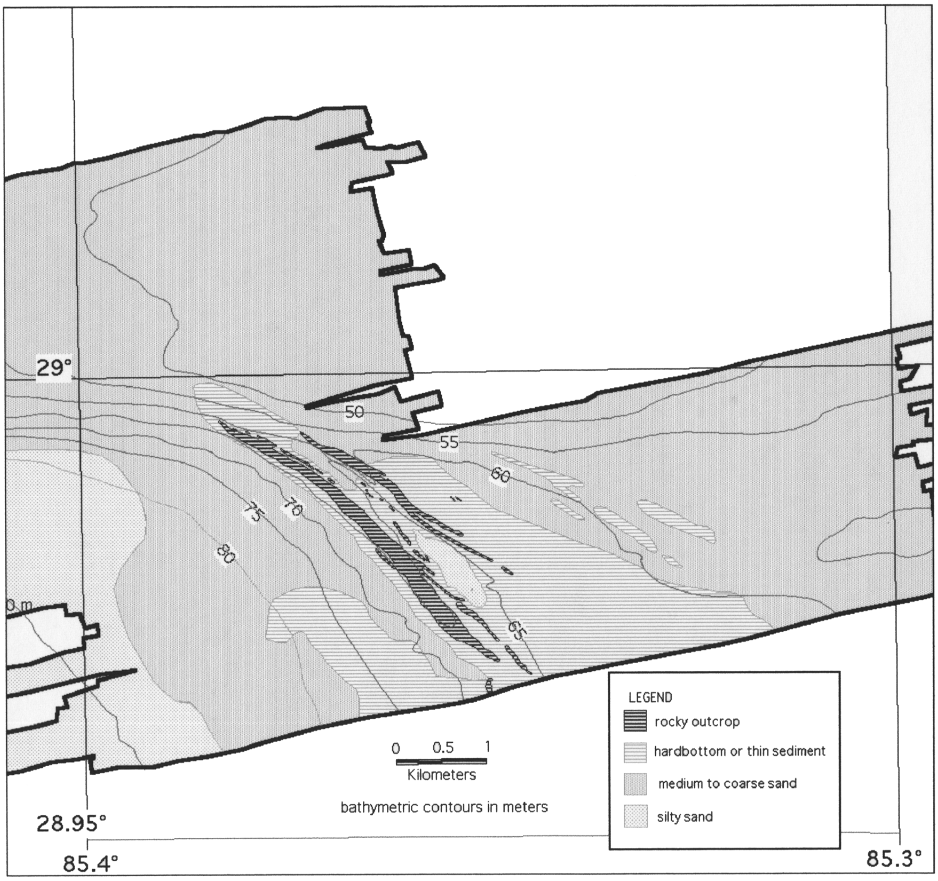

Figure 5. Map of Twin Ridges on the west Florida shelf showing locations of rocky ridges, hard bottom, and sandy sediments.

storms or high currents, then the living, intact *Oculina* on Jeff's Reef and the toppled and broken *Oculina* coral heads elsewhere would have been removed as well. Our contention that trawling caused the *Oculina* habitat destruction is also supported by the public testimony to the South Atlantic Fishery Management Council by local rock shrimpers, who attest to the abundance of rock shrimp associated with the coral and their use of the area as fishing grounds.

The extent to which damaged coral habitat can be restored is of considerable interest to ecologists, particularly in light of the marked decreases in live coral coverage known to occur throughout tropical and subtropical seas (Hughes, 1994). Although these large-scale declines are more often attributed to global warming (e.g., by Ware, 1997) and disease (e.g., by Santavy and Peters, 1997) than to mechanical degradation, the same impetus exists to stop and reverse them. That is, habitat structure is so fundamentally important to biodiversity and biomass production (Fletcher and Underwood, 1987; Walters and Wethey, 1996) that its loss profoundly affects ecosystem function.

Coral restoration is being evaluated for reefs throughout the world. The two principal methods are seeding, in which larvae or young recruits are distributed throughout a dam-

Table 9. Percent composition of reef fish species videotaped with an ROV on Twin Ridges reef of the west Florida shelf in the spring of 1997 (n = 260). Economically important species are marked with asterisks.

Species		Percentage
Blue angelfish	*Holacanthus bermudensis*	13.82
Red snapper*	*Lutjanus campechanus*	13.01
Scamp*	*Mycteroperca phenax*	11.38
Red barbier	*Hemanthias vivanus*	8.13
Red porgy*	*Pagrus pagrus*	7.72
Amberjack*	*Seriola* sp.	6.91
Yellowtail reeffish	*Chromis enchrysurus*	5.69
Cubbyu	*Equetus umbrosus*	4.88
Short bigeye	*Pristigenys alta*	4.88
Porgy*	*Calamus* sp.	3.66
Reef butterflyfish	*Chaetodon sedentarius*	3.25
Greater amberjack*	*Seriola dumerili*	3.25
Butterflyfish	*Chaetodon* sp.	2.44
Grouper*	*Mycteroperca* sp.	2.44
Bank butterflyfish	*Chaetodon aya*	1.63
Wrasse	*Halichoeres* sp.	1.63
Creole fish	*Paranthias furcifer*	1.22
Tattler	*Serranus phoebe*	1.22
Spotfin butterflyfish	*Chaetodon ocellatus*	0.81
Spanish flag	*Gonioplectus hispanus*	0.81
Red grouper*	*Epinephelus morio*	0.41
Wrasse bass	*Liopropoma eukrines*	0.41
Almaco jack*	*Seriola rivoliana*	0.41

aged reef, and transplant, in which intact fragments of living coral are moved to damaged sites (Tunnicliffe, 1981; Alcala et al., 1982; Gittings et al., 1988; Birkeland and Lucas, 1990). Preliminary in situ experiments conducted in the EORR from 1996 through 1999 to evaluate the potential for *Oculina* coral restoration indicate that transplantation is the most practicable, in part because local recruitment occurs so much more slowly (Koenig, unpubl. data). Because the growth rate of intact *Oculina* is roughly 16 mm yr^{-1} (Reed, 1981), restoration to about meter-size colonies could occur in about 30 yrs, if the sites remain protected. In fact, these data suggest that closed areas can serve as extremely important tools in evaluating and effecting recovery of habitats degraded by destructive fishing practices.

West Florida.—Ecological communities, habitat, and ecosystem function on continental shelf areas are probably very different now than they were a century and a half ago. Certainly the fisheries have changed dramatically in that time. The red snapper (*Lutjanus campechanus*) fishery, which was concentrated along the west Florida shelf edge in the late 1800s after shallower stocks declined (Collins, 1887), is a small remnant of what it was, according to descriptions by early sea captains in the fishery (Camber, 1955). It persists primarily in the western Gulf of Mexico, much of it associated with the nearly 6000 oil and gas platforms and numerous artificial reefs that dot the region (Goodyear, 1995).

Table 10. Relative abundance of species captured during at-sea sampling on commercial vessels by the National Marine Fisheries Service Panama City Laboratory on the west Florida shelf edge.

Species		Percentage
Gag	*Mycteroperca microlepis*	32
Red porgy	*Pagrus pagrus*	24
Red grouper	*Epinephelus morio*	18
Scamp	*Mycteroperca phenax*	17
Red snapper	*Lutjanus campechanus*	4
Gray snapper	*Lutjanus griseus*	4
Vermilion snapper	*Rhomboplites aurorubens*	1
Lane snapper	*Lutjanus synagris*	1

With the exception of red snapper, the vast majority of reef fish harvested in the Gulf of Mexico are captured in the eastern region (Moe, 1963; NMFS, 1997). These reef fish are an extremely important economic resource, comprising the major target of marine fishing and generating billions of dollars annually in the state of Florida (Bell, 1993). Commercial hook-and-line and longline fishers concentrate on reef fish on the shelf edge, whereas recreational fishermen typically fish shallower shelf reefs.

Even though the shelf-edge habitat figures prominently in fishery production for the entire region (particularly for species like gag and scamp), we know virtually nothing about its function and very little about its structure. For example, no studies have addressed the direct effects of fishing on habitat structure on west Florida shelf-edge reefs, even though trawling, dragging anchors, and other potentially damaging fishing practices occur. Information on indirect effects of fishing on habitat is also lacking. An essential first step in exploring these problems is detailed mapping of geological features, an activity still in its infancy in this region. In fact, the only high-relief reef system of the west Florida shelf mapped and characterized before our study was the Florida Middle Grounds (see, e.g., Smith et al., 1975; Darnell, 1990). We hope to remedy this situation by continuing our mapping efforts throughout the west Florida shelf region through collaborations with NOAA and the USGS.

Fish Communities and the Effects of Fishing

Fish Species Diversity, Abundance, and Biomass.—The information we have about the EORR essentially represents snapshots taken before (1980) and after (1995–1998) heavy fishing took place in the area. In addition, we can consider the work reported here to be baseline information on the condition of the EORR prior to closure. The work we have conducted since that time can therefore tell us much about the effects of closure.

We realize that our conclusions are tentative, given the lack of replicated samples and parallel controls and the quantification of fish abundance on the basis of temporally distinct images collected for different scientific purposes. Nevertheless, the differences over time at in the same site and among habitats at the same time are so striking that they leave little room for doubt—fishing has had an enormous effect on both habitat and community structure. Given the logistic challenges of sampling in the Florida Current during seasonally harsh weather conditions at sea, at depths that preclude use of SCUBA, the mere detection of differences testifies to their magnitude.

Fish species diversity on Jeff's Reef appeared higher in 1995, after years of heavy fishing, than it did in 1980. Whether real or due to sampling artifacts, this change probably results from the removal of predators like gag and scamp. In structurally complex habitats like Jeff's Reef, small fishes tend to be cryptic and to hide within the many interstices of coral heads when large, piscivorous fishes are present. In the absence of piscivores, small fishes may be both less inclined to hide, and thus more conspicuous in censuses, and more abundant, because their numbers are not depleted by piscivory. W. J. Lindberg (University of Florida, pers. comm.) found an inverse relationship between gag abundance and prey abundance on artificial reefs, so smaller fish species may become seasonally depleted on sites where seasonal aggregations occur.

The expected and observed fish species diversity differed considerably on several reefs sampled in 1995 (Table 7). At Chapman's Reef and the Steeple, both damaged sites, the observed diversity was 24% lower than expected; at Twin Peaks, a destroyed site, it was 35% lower. Observed and expected diversity did not differ at Sebastian Pinnacles, apparently because of the structural complexity provided by fissures and solution holes in the base rock. We found that diversity was greatest around such structure even though the *Oculina* habitat was completely destroyed.

The intact, structurally complex habitat of Jeff's Reef had nearly twice the diversity seen on the four damaged reefs, and diversity there may have been even higher, as many cryptic species may not have been apparent on the videotape. The more complex the habitat, the greater the chance that diversity will be underestimated. By the same token, characteristically cryptic species would have been observed in the destroyed habitat if they were present.

Numbers and biomass of economically important reef fish on Jeff's Reef showed striking differences between 1980 and 1995, on the basis of our limited data sets (Fig. 3A,B). Nearly 70% of the dominant species in 1980 were economically important species, mostly aggregating groupers (Table 1). The loss (gag) and diminution (scamp) of these aggregations accounted in large part for the observed changes. Because these aggregations are composed of migrants from distant locations (Gilmore and Jones, 1992; Van Sant et al., 1994), the decreases probably reflect regional population reductions.

Fishers concentrate on spawning aggregations because the aggregations are predictable—that is, they are consistent in space and time—and because doing so greatly increases catch per unit effort (see, e.g., Olsen and LaPlace, 1979; Sadovy, 1990; Koenig et al., 1996; Domeier and Colin, 1997; Johannes et al., 1999). Acute effects of aggregation fishing include the total loss of aggregations; chronic effects may include deterioration of reproductive capacity and altered genetic composition of the stock. In either case, ample evidence shows that aggregation fishing rapidly undermines sustained fishery production (Coleman et al., 1996; Beets and Friedlander, 1999; Sadovy and Eklund, 1999). The synergy of the life history traits of protogyny and aggregation spawning appears to increase dramatically the vulnerability of reef species to overfishing when effort is concentrated on spawning fish (Coleman et al., 1999; Johannes et al., 1999).

CASE STUDY: GAG

Concern about the effects of fishing on the health of gag stocks in both the eastern Gulf of Mexico and the South Atlantic arose from studies showing significant declines in the apparent proportion of males over a 15-yr period (late 1970s to mid 1990s; Coleman et al., 1996; McGovern et al., 1998). We use the term 'apparent' simply because the data are fishery-dependent and the underlying or absolute proportions are unknown. On the basis of data sets separated by gear type, area, and season, we found that the historic percentages of males during the spawning-aggregation period (December to March) were 15% in the Gulf and 11% in the Atlantic and that the percentages declined significantly ($P < 0.01$) over time to about 2 and 5%, respectively. Because sex change occurs near the time of aggregation (most transitionals were observed just after aggregation), the cues for sex change are probably restricted to that time. Because, further, no evidence supports either size or age control of sex change, the transition is probably socially mediated (and size important secondarily; Warner, 1988), and fishing probably disrupts the sex-change process. Other changes in the gag population over the same period include a loss of spawning aggregations (Koenig et al., 1997), a decrease in size at maturity (McGovern et al., 1998), and a general decrease in mean size (Coleman et al., 1996). There is also evidence of inbreeding in the gag population (Chapman et al., 1999), possibly resulting from a low proportion of males.

The link between increased fishing pressure and male decline has been clearly and repeatedly demonstrated (Schirripa and Goodyear, 1994; Coleman et al., 1996; Koenig et al., 1996; Schirripa and Legault, 1997; McGovern et al., 1998). Further, although peak catches occur during the spawning season (Koenig et al., 1996), male capture increases on shelf-edge reefs in the postaggregation period (Koenig, unpubl. data). These results strongly suggest that shelf-edge fishery reserves are necessary to manage the gag fishery and to ensure optimum reproductive capacity. In that regard, gag can be considered a flagship species (sensu Towns and Williams, 1993) for other economically and ecologically important reef fish, many of which use shelf-edge reefs for spawning and some of which respond to fishing in a manner similar to gag. Scamp is a case in point (Coleman et al., 1996), as is red porgy (*Pagrus pagrus*). For red porgy, in fact, the population has declined so dramatically in the South Atlantic Bight over the last 20 yrs, regardless of the traditional management restrictions imposed (Vaughan et al., 1992; Harris and McGovern, 1997), that the fishery recently collapsed (Vaughan, 1999).

For protogynous aggregating species, only year-round no-take reserves protect the integrity of spawning aggregations (i.e., the sex-change process and the social structure), the population size structure, and under the same umbrella, the habitat and associated species. Although management outside of closed areas is still required, reserves do to some extent simplify regulation. Seasonal closures for single species of reef fish, for example, fail because these species occur in complexes rather than in isolation. As fishers pursue capture of allowed species, they increase their regulatory discard of protected ones, and because capture-release mortality in shelf-edge or shelf-slope areas is near 100%, the overall protection afforded is likely to be nil. In addition, management regimes are likely to become even more complex if seasonal closures are deemed necessary for all protogynous aggregating species (which, in addition to gag, include scamp; red porgy; black grouper, *Mycteroperca bonaci*; jewfish, *Epinephelus itajara*; Nassau grouper, *Epinephelus striatus*; and possibly the deep reef complex of snowy grouper, *Epinephelus niveatus*; Warsaw grouper, *Epinephelus nigritus*; speckled hind, *Epinephelus drummondhayi*; and yellowedge grouper, *Epinephelus flavolimbatus*). Our knowledge of the reproductive ecology of any of these species is poor, but the effects of shelf-edge fishing on gag (as well as scamp and red porgy) strongly suggest that shelf-edge reserves are required if these species are to continue production.

In the vast majority of cases, the potential contribution of marine fishery reserves to fishery production is unknown. The tendency is to attempt to model the characteristics of reserve networks from what is known about fished populations and the altered communities and habitats that support them, but in fact, these models are little more than educated guesses. Community changes and productive outputs that may result from closing a significantly large area cannot be anticipated. If marine fishery reserves enclose reproductive groups, like grouper spawning aggregations, the benefits from closure of a relatively small proportion of the fished area could be enormous, because of the huge reproductive potential of these species and because it is unknown how many spawning aggregations can develop within a specified area. We therefore feel it is imperative that experimental marine fishery reserves be established in systems such as shelf-edge habitats so that researchers can develop some concept of the production trajectory of protected populations. The size and location of reserve networks can then be based on the relatively firm ground of experimentation.

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