BULLETIN OF MARINE SCIENCE, 43(2): 280–307, 1988

REEF FISH ASSEMBLAGES ON HARD BANKS IN THE NORTHWESTERN GULF OF MEXICO

George D. Dennis and Thomas J. Bright

ABSTRACT

SCUBA diver and submersible observations were used to characterize tropical reef fish assemblages on the hard banks of the northwestern Gulf of Mexico, which have been relatively unstudied due to their remoteness and depth. Four assemblages were distinguishable: coral reef, mid-shelf, algal-sponge, and drowned reef zones in the order of their species richness. These tropical communities are limited to the intermediate and outer shelf by winter cooling of inner shelf waters and high turbidity associated with discharge of the Mississippi/Atchafalaya and other rivers. These communities exhibit seasonal stability and annual persistence over the length of the study (ca. 10 yrs).

High reef fish diversity at the Flower Garden banks is due to the variety of habitats and insular environmental conditions. Some Caribbean species are not established in the northwestern Gulf due to the lack of habitat diversity rather than temperature tolerance.

Similarities in reef fish species composition on widely scattered banks is due to similar crest depths and hydrographic conditions which result in similar epibenthic communities. The nepheloid layer was the most important environmental factor in determining composition of reef fish assemblages, by producing low species richness and abundance. Limited food resources may also play a role in determining reef fish abundance and species composition on deeper reefs. The scarcity of hard substrate and the presence of the nepheloid layer combine to limit the distribution and abundance of tropical reef fish in the northwestern Gulf of Mexico.

Species composition of tropical reef fish assemblages indicate an ecotone between western Atlantic continental and insular tropical faunas in the northwestern Gulf of Mexico.

The marine fauna of the northwestern Gulf of Mexico has generally been considered a disjunct component of the warm temperate Carolinian biogeographical province (Hedgpeth, 1953; Briggs, 1974) and the region is known for its extensive soft bottom continental shelf communities (Chittenden and McEachran, 1976). Several researchers have recognized the existence of a tropical faunal component in the region (Caldwell, 1959; Dawson, 1962) but believed it to be expatriated from the Caribbean. Tropical fauna is limited in its distribution by the scarcity of suitable hard bottom habitats in the northwestern Gulf. However, high relief banks harboring an extensive tropical reef biota, occur in the region as islands of hard substratum surrounded by vast expanses of terrigenous continental shelf sediments (Bright, 1977).

The hard banks of the northwestern Gulf have been well known by commercial fishermen since the 1890's for their concentrations of red snapper (Camber, 1955). Yet only in the past 20 years has the extent of the tropical fauna inhabiting them been substantially documented (Bright and Pequegnat, 1974; Sonnier et al., 1976; Rezak et al., 1985).

Submersible and SCUBA observations collected on the offshore hard banks of the northwestern Gulf of Mexico were used to describe the taxonomic composition and abundance of reef fish inhabiting the region and to compare similar habitats in the Gulf of Mexico and Caribbean.

Description of Study Area

The offshore topographic features of the northwestern Gulf of Mexico can be divided into three groups based on their surface geological expression: banks with growing carbonate reefal caps over bedrock (shelf-edge banks), non-carbonate tertiary bedrock banks (mid-shelf banks), and mid-shelf relict Pleistocene algal reefs (south Texas fishing banks). The area of major relief for each bank is listed in Table 1.

Hydrographic parameters are similar on the mid- to outer shelf, where the hard banks are located. Although the discharge of the Mississippi and Atchafalaya rivers influences salinities on the inner shelf of the northwestern Gulf, there is little effect on bottom salinity at depths greater than 30 m, where salinities are rarely less than 36‰ (Harrington, 1966). Two hydrographic factors, temperature and turbidity, are important on this part of the shelf. Water temperatures, which vary considerably with depth, are described below for each bank group. The northwestern Gulf continental shelf is characterized by a turbid bottom water layer known as the nepheloid layer. The nepheloid layer is attributable to fine silts and clays discharged primarily by the Mississippi and Atchafalaya rivers (Griffin, 1979). The depth of the nepheloid layer at each bank is reported in Table 1. The following bank descriptions are summarized from Rezak et al. (1985) which may be referred to for more detailed information.

Shelf-edge Banks.—Sixteen banks extending from the West Flower Garden SSE of Galveston, Texas, to Sackett bank near the Mississippi River Delta make up a set of carbonate platforms which have formed on top of diapric salt intrusions along the continental shelf edge and are collectively known as the shelf-edge banks (Fig. 1). The crest depth of each bank determines the number of biotic zones associated with it. The East and West Flower Garden banks (EFG and WFG) are special forms of shelf-edge banks because their exceptionally shallow reef crests allow the development of a high diversity hermatypic coral reef community, the *Diploria-Montastrea-Porites* zone (15–36 m) (Bright et al., 1984). A low diversity hermatypic coral reef zone dominated by *Stephanocoenia* and *Millepora* occurs below this at the Flower Gardens, and on the crests of Bright and 18 Fathom banks between 36- and 52-m depth. The remaining shelf-edge banks are characterized by reef crests at depths greater than 50 m and possess only two epifaunal biotic communities, the algal-sponge and Antipatharian zones (Rezak et al., 1985) (Table 1) (Fig. 2). The algal-sponge zone is dominated by crustose coralline algae primarily in the form of rhodoliths (algal nodules). Patches of reef rock known as "partly drowned reefs" within this zone are typically encrusted with coralline algae. Sponges are common, including large colonies of *Neofibularia nolitangere* and massive demosponges. This zone occurs from 45 m to as deep as 98 m. In the deeper portion of this depth range there is a transition from the algal-sponge zone to a zone characterized by large populations of antipatharian sea whips (Antipatharian zone) (Fig. 2).

Antipatharians extend down into the nepheloid layer through which most of the banks project. The depth of the nepheloid layer is variable but usually occupies the bottom 10 to 20 m of the water column (Table 1). Within the nepheloid layer hard substrates are composed of "drowned" algal reefs, encrusted with sponges and other turbidity-tolerant epifauna. The surrounding sediments are primarily terrigenous soft bottom as is typical of the region.

Two banks surveyed in this study, Coffee Lump and Fishnet, are considered transitional based on their intermediate position on the shelf between the mid-shelf and shelf-edge banks. Periodically, due to the low relief of their crests these banks are completely enveloped in the nepheloid layer.

The shelf-edge banks offer insular environmental conditions to tropical organisms due to the buffering effect on temperature fluctuations by the deep Gulf waters and the limited exposure to turbid water conditions. Similar conditions are found on Caribbean islands without extensive continental shelves. The shelf-edge banks still receive greater seasonal temperature fluctuations than most Caribbean locations due to winter cooling of inner shelf waters.

In the upper 50 m of the water column on the shelf-edge banks temperatures below 20°C have been reported from mid-December to April with an annual range from 19 to 30°C (Rezak et al., 1985). Between 50- and 80-m depth, water temperature ranges from 17 to 26°C. Below 80 m bottom water temperatures range from 16 to 22°C. Offshore bottom waters reach a minimum in February (Harrington, 1966).

Mid-shelf Banks.—The mid-shelf banks, represented in this study by Claypile, Sonnier, and Stetson banks, arise from surrounding depths of less than 64 m (Fig. 1) (Table 1). These banks are associated with salt diapirs and have exposed Tertiary claystone/siltstone outcrops rather than carbonate reef caps. The biotic community occupying these banks is the *Millepora*-Sponge zone, dominated by the fire coral *Millepora alcicornis* and sponges such as *Neofibularia* and *Ircinia* (Fig. 2). The hermatypic coral *Stephanocoenia michelini* occurs here but is rare.

Water clarity is generally, but not always, high at the relatively shallow crests of Stetson and Claypile banks. The shallower surrounding depths at these banks allow storm-induced turbidity to cover the banks entirely from top to base at times. In addition, the deeper crest of Claypile is more frequently enveloped in the nepheloid layer than the crest of Stetson. Bottom water temperatures range from a high in the summer (August) of 29°C to a winter (February) minimum of 16°C.

Table 1. Location of the offshore hard banks with information on their crest depth, shallowest depth of the nepheloid layer, surrounding bottom depths, area of elevated bottom, number of hours of submersible survey time, number of species (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J'). Depth measured in meters and area in square kilometers. Latitude and Longitude reported in degrees and minutes

	Latitude (N)	Longitude (W)	Crest depth	Neph. depth	Surr. depth	No. h surveyed	Area	S	H'	J'
Mid-shelf Banks										
Claypile	27°19'	94°09'	40	45	50	3.27	6.12	36	1.457	0.406
Sonnier	28°20'	92°27'	18	52	60	2.17	0.78	25	1.400	0.435
Stetson	28°10'	94°18'	20	52	55	4.47	0.27	43	1.909	0.508
South Texas Fishing Banks										
Aransas	27°35'	96°27'	57	70	70–72	2.13	0.50	16	1.527	0.551
Baker	27°45'	96°14'	56	70	70–74	1.62	1.33	20	1.549	0.517
Dream	27°03'	96°42'	62	70	80	3.00	2.39	20	1.466	0.489
Hospital Rock	27°33'	96°29'	59	70	70–78	6.90	2.77	24	1.373	0.432
North Hospital	27°34'	96°29'	58	70	68–70	1.27	1.65	12	1.287	0.518
South Baker	27°41'	96°16'	59	70	80–84	1.28	0.31	22	1.458	0.472
Southern	27°26'	96°31'	58	70	80	4.78	1.07	22	1.464	0.474
Shelf-edge Banks										
Alderdice	28°05'	91°60'	55	82	84–90	3.98	11.45	32	1.267	0.366
Bouma	28°02'	92°27'	60	84	90–100	3.50	13.97	26	1.457	0.447
Bright	27°53'	93°18'	37	P*	110	7.40	16.67	36	1.457	0.407
Diaphus	28°05'	90°42'	73	98	110–130	3.82	7.19	22	1.508	0.488
East Flower Garden	27°54'	93°36'	15	86	100–120	67.45	42.28	79	2.153	0.493
Elvers	27°50'	92°54'	60	123	180	5.80	26.34	31	1.646	0.479
Ewing	28°06'	91°02'	56	80	85–100	3.33	14.03	27	1.663	0.505
Geyer	27°51'	93°04'	37	123	190–210	10.65	41.23	48	1.721	0.445
Jakkula	27°59'	91°40'	59	98	120–140	2.57	3.60	20	1.464	0.489
Rezak-Sidner	27°57'	92°23'	55	100	120–150	3.68	29.23	24	1.492	0.469
Sackett	28°38'	89°33'	67	85	100	4.73	7.02	28	1.463	0.439
West Flower Garden	27°52'	93°48'	20	89	110–130	23.13	41.29	72	1.856	0.434
18 Fathom	27°58'	92°36'	45	P*	110–130	4.38	8.01	45	1.582	0.416
28 Fathom	27°55'	93°27'	52	100	110–140	11.25	80.30	38	1.647	0.453
Transitional Banks										
Coffee Lump	28°05'	93°55'	60	60	68–75	7.00	2.65	22	1.680	0.543
Fishnet	28°09'	91°48'	60	60	78	3.87	1.30	25	1.530	0.475

P* = indicates nepheloid layer present but depth not determined.

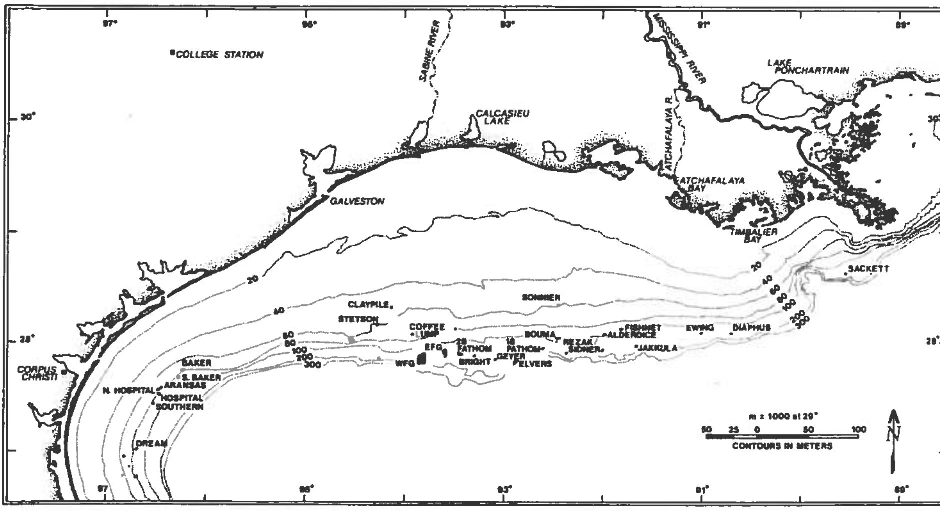

Figure 1. Hard banks of the northwestern Gulf of Mexico.

South Texas Fishing Banks.—The south Texas fishing banks (STFB) comprise 11 topographic features which are situated in surrounding water depths of 69 to 84 m (Fig. 1). The hard substrata that form these banks are low relief, drowned, late-Pleistocene algal reefs projecting upward from a relict carbonate shelf which is not associated with salt diapirs.

The primary epibenthic community is a low diversity faunal assemblage, the Antipatharian zone, which predominates on these banks down to 70 m, the usual top of the nepheloid layer (Fig. 2). Reef crests are no shallower than 55 m and waters at this depth are turbid much of the time due to the temporally varying thickness of the nepheloid layer (Table 1).

Bottom water temperatures in this area range from 17°C (February) to 23°C (August).

Methods and Materials

Most research on reef fish precludes the use of standard fish collection methods such as trawls or seines except where the habitat relief is low (Miller and Richards, 1979; Powles and Barans, 1980; Wenner, 1983). The use of hook-and-line catch surveys of reef areas are usually biased toward larger fish (Grimes et al., 1982). Tropical reef fish are particularly well suited to visual observation due to their distinctive coloration and the clarity of their underwater habitat. The development of SCUBA has greatly enhanced the research carried out on coral reefs but is practically limited to depths less than 45 m (Starck, 1968; Itzkowitz, 1974; Gladfelter et al., 1980). For surveys of reef fish at greater depths, research submersibles and/or towed camera systems have afforded the best non-destructive techniques (Colin, 1974; 1976, off several Caribbean islands; Avent et al., 1977, off the eastern Florida coast; Shipp and Hopkins, 1978, off the north central Gulf of Mexico; and Jones and Clark, 1981, off the Florida Keys).

Reef fish abundance and distribution data were obtained from visual observations made along transects traversed by the Texas A&M University submersible Diaphus on 26 hard banks in the northwestern Gulf of Mexico. Dives used in our analysis were made diurnally during the summer/fall seasons, usually from the reef crest down slope until no further hard substratum was encountered. The observational data were recorded within the submersible on color or black-and-white video tapes with simultaneous audio notes by the dive scientist (T.J.B.). The video tapes were reviewed in the laboratory and fish were identified to the lowest possible taxon and were enumerated by depth. For the purpose of analysis, raw abundance values were grouped into 5-m depth intervals.

Although the area surveyed during a submersible transect could not be accurately estimated due to the nature of the transects (neither straight nor traversed at a constant speed) the proportion of time spent in each depth zone was calculated to obtain comparable quantitative abundance values expressed as the number of fish per survey hour. These values are felt to adequately depict the depth-abundance relationships within a taxon but are more approximate for between taxa comparisons (Bright et al., 1984). On banks with shallow crest depths (<35 m), qualitative observations on reef fish were obtained by SCUBA divers, supplementing submersible observations. Data on seasonal occurrence of reef fish

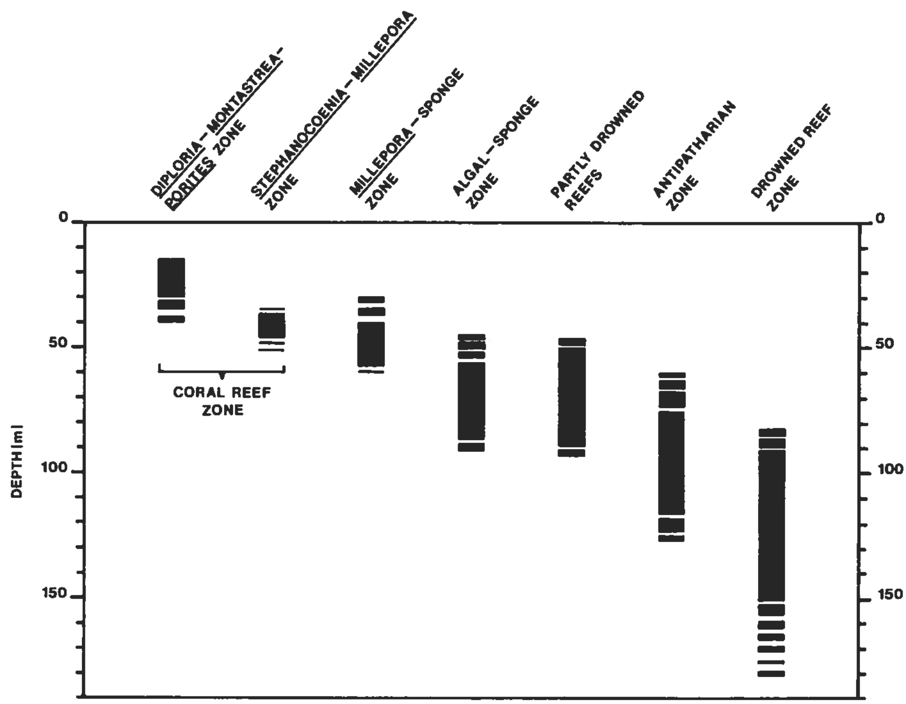

Figure 2. Biotic zones known to occur on the hard banks of the northwestern Gulf of Mexico. Broken bar indicates varying upper and lower depth limits depending on location.

were acquired from quarterly SCUBA surveys at the Flower Garden banks from 1978 to 1981 by the senior author. All species and common names of reef fish used in this paper follow the recommendations of Robins et al. (1980).

For community analysis, raw abundance data were standardized by total number of individuals per unit time within a depth range or taxon (Clifford and Stephenson, 1975). Rare taxa which occurred at two banks or less were excluded from the numerical analysis. The standardized abundance data were used in Bray-Curtis ordination to calculate ecological distances for 5-m depth intervals and taxa (species) for the following locations: West Flower Garden (WFG), East Flower Garden (EFG), EFG and WFG combined, and all banks combined (Field et al., 1982; Gauch, 1982). Clustering analysis was employed using an agglomerative hierarchical strategy with flexible sorting ($\beta = -0.25, \alpha = 0.625$) to generate both normal and inverse classifications (Clifford and Stephenson, 1975). The Ecological Analysis Package (EAP) implemented on the Statistical Analysis System (SAS) was run on an AMDAHL 470 computer at the Texas A&M University Data Processing Center to generate the Bray-Curtis ordinations and clustering analyses. Each classification was selectively divided into groups for nodal analysis to express the degree of depth interval and species group coincidence. The nodal analysis was used to interpret the constancy and fidelity of species groups for particular depth groups (Boesch, 1977).

Constancy is used to express the degree to which a species group occurs within a depth group. This index ranges from 1, where all species occur in all depth intervals within a depth group, to 0, where no species occur within that depth group. Constancy indices are graded from high to low to more graphically depict relationships (Boesch, 1977).

$$C_{ij} = a_{ij}/(n_i n_j)$$

C_{ij} = constancy of species group i in depth group j, a_{ij} = number of taxa of species group i in depth group j, n_i = number of taxa in species group i and n_j = number of depth intervals in depth group j.

Fidelity indices are developed from the ratio of constancy of a particular species-group/depth-group combination to overall constancy of that species group. This index attempts to convey an indication of depth group preference (and habitat faithfulness) for a particular species group. High to moderate fidelity (≥ 2) is indicative of a species group's "preference" for a depth group while index values less than one suggest "avoidance" of the depth group by those species (Boesch, 1977).

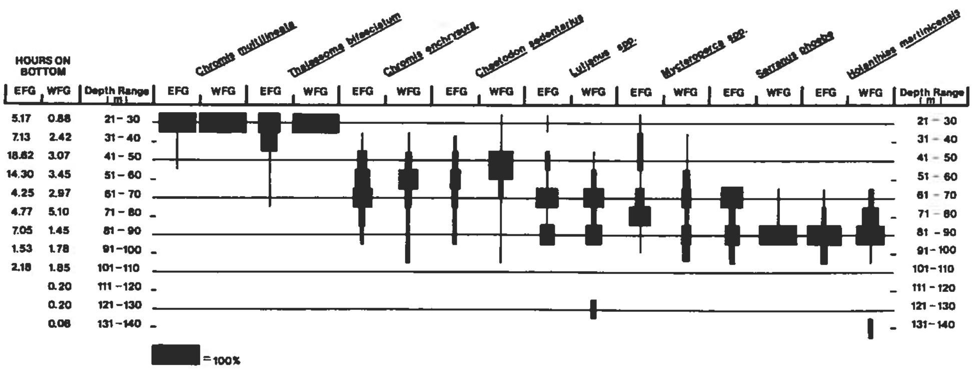

Figure 3. Abundance with depth of selected reef fish within each reef fish assemblage based on the number of individuals observed per hour survey time and expressed as a percentage of the total number for that species.

$$F_{ij} = a_{ij}\ \Sigma\ n_j/n_j \cdot a_{ij}$$

F_{ij} = fidelity of species group i in depth group j, a_{ij} = number of taxa of species group i in depth group j and n_j = number of depth intervals in depth group j.

Because submersible observations were considered to be a sample of the total population, the Shannon-Wiener (H′) diversity index (natural log) was calculated for each reef fish assemblage (Pielou, 1975).

$$H' = -\Sigma\ p_i \ln\ p_i$$

H′ = index of species diversity and p_i = proportion of the total sample belonging to the i species. The diversity indices were used for comparative purposes within our data set and were based on submersible observations only. Since the diversity indices were based on a small sample size, the Kruskal-Wallis test (the nonparametric equivalent of ANOVA) was used to compare diversity indices among bank groups (Daniel, 1978). Evenness (J′) was calculated as $J' = H'/\ln S$ and species richness (S) as simply the total number of species in a reef fish assemblage or at a bank (Pielou, 1975).

Primary reef fish are defined here as those which are characteristically associated with reefs or hard substrates (Starck, 1968). The relative abundance of each species by fish assemblage is tabulated in Appendix Table 1. The following categories are used to represent the abundance of reef fish species based on the cumulative data of diver, video, and photographic observations: present—known present but not enough information to evaluate abundance, rare—less than three individuals observed within a fish assemblage, occasional—species observed at irregular intervals, frequent—species observed in a high proportion of the samples, common—ubiquitously present in samples but not numerous, and abundant—numerous individuals observed in all samples within a fish assemblage. These abundance categories are applied both within a fish assemblage (e.g., coral reef zone) or within a bank group (e.g., shelf-edge banks), thus a species may be abundant at a particular bank but if not found at other banks within a bank group it would be only occasional for that bank group. See Dennis (1985) for information on the abundance of reef fishes at each bank and an annotated list of species.

Results

Flower Garden Banks.—Few submersible observations were available above 30 m at the Flower Garden banks, but the area has been surveyed qualitatively using SCUBA. The coral reef zone has similar species composition to that reported by Bright and Cashman (1974) for the WFG. A SCUBA visual census in 1972 recorded three dominant fish species (Bright et al., 1974): *Chromis multilineata* (brown chromis), *Thalassoma bifasciatum* (bluehead), and *Clepticus parrai* (creole wrasse). Similar dominance by these species was noted at both the EFG and WFG in our study (Fig. 3), with some additions. *Paranthias furcifer* (creole-fish) and *Clepticus parrai* formed tremendous mixed feeding schools in midwater above

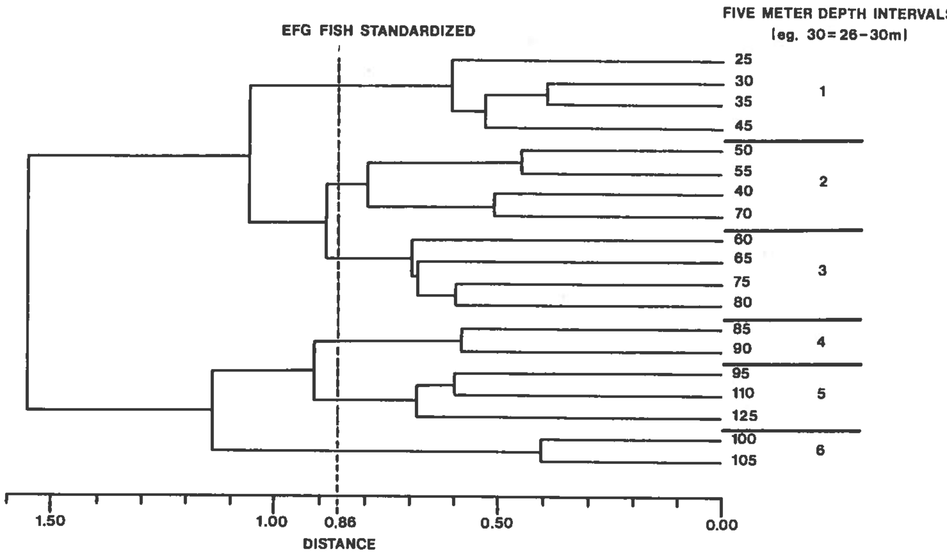

Figure 4. Clustering results of 5-m depth intervals at the East Flower Garden bank with nodal analysis groups marked. Depth interval equals 21–25 and so on.

the reef crests of both banks. Territorial pomacentrids, *Pomacentrus planifrons* (threespot damselfish) and *Pomacentrus partitus* (bicolor damselfish) were common on the coral reef along with *Bodianus rufus* (Spanish hogfish), *Epinephelus adscensionis* (rock hind), and *Epinephelus cruentatus* (graysby). The relative abundances of other coral reef fish are listed in Appendix Table 1.

At depths greater than 30 m there were sufficient submersible observations to numerically classify the deeper portion of the coral reef zone. The EFG and WFG banks were quite similar in depth classification, but a 5 to 10 m difference in surrounding depths between the two banks confounded the depth classification of the combined data sets. Therefore, the analysis of the larger EFG dataset is used as representative of the numerical analysis of depth and species composition for both banks. Differences between the two banks will be illustrated where necessary.

Figure 4 depicts the Bray-Curtis clustering of 5-m depth intervals at the EFG. At both banks the shallowest depth group (1), composed of depths less than 45 m, was found to represent the coral reef zone. Figure 5 shows the inverse classification of submersible-observed reef fish at the EFG. Nodal analysis (Figs. 6a, b) demonstrates that species groups V through X are representative of the coral reef zone, but only two groups (VIII and X) exhibited even moderate fidelity (Fig. 6b) to this zone. Group X possesses many of the species commonly observed by SCUBA at shallower depths on the coral reef. One hundred and twelve species have been visually observed above 45 m at the Flower Garden banks (Appendix Table 1). Based solely on submersible observations, Shannon-Wiener diversity (H′) for the fish assemblage in depths less than 45 m was 1.761 for the EFG and 1.460 for the WFG (Table 2).

Depth groups 2 and 3 form a closely associated set delimiting the algal-sponge zone (Fig. 4). All species groups were represented in this depth range but only two groups (II and VII) showed both moderate to high constancy and fidelity (Figs. 6a, b). Species such as *Chromis enchrysura* (yellowtail reeffish), *Chaetodon*

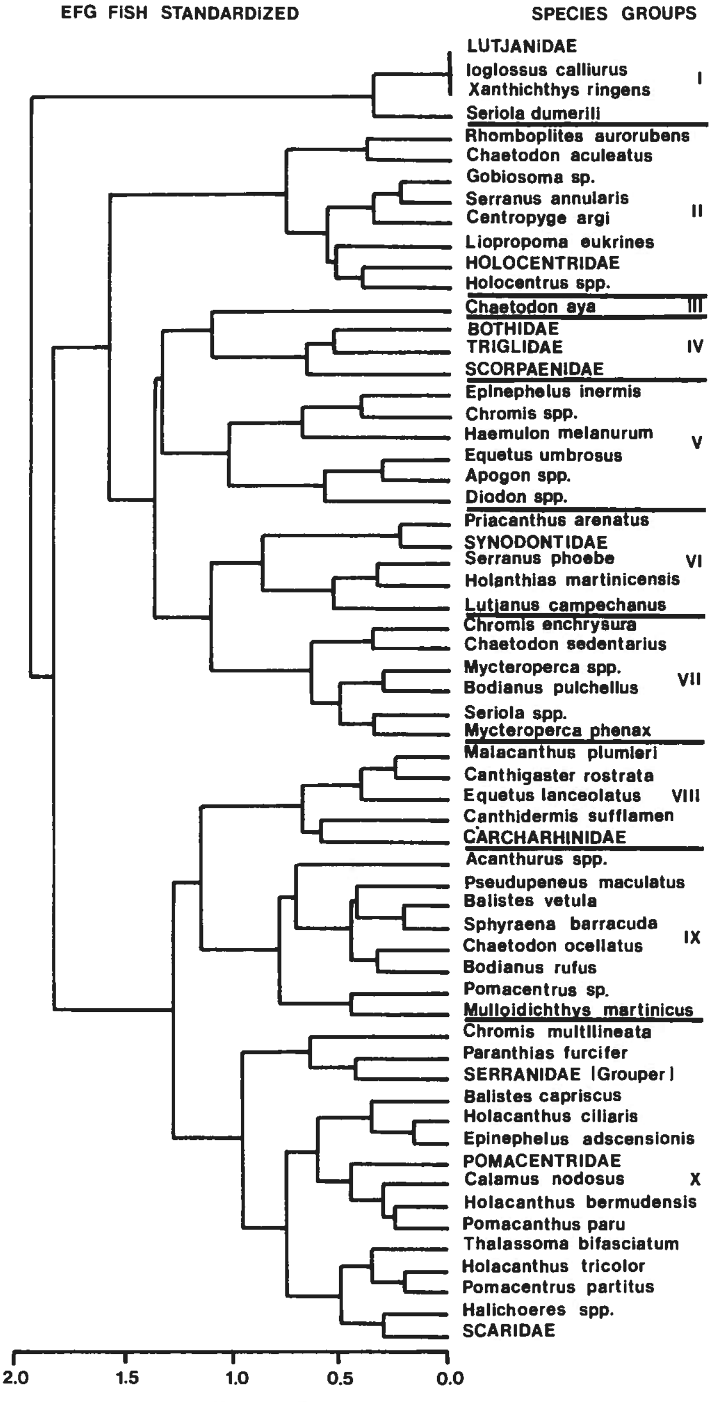

Figure 5. Inverse classification of species groups at the East Flower Garden bank.

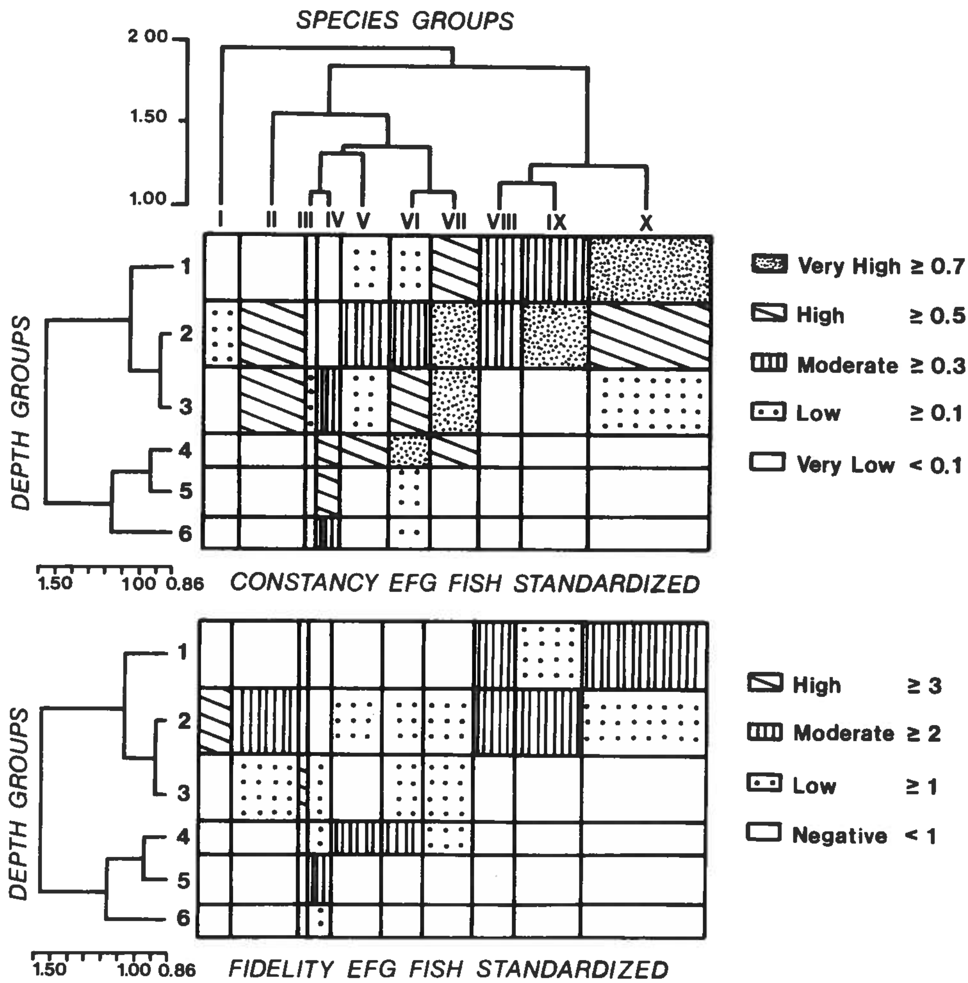

Figure 6. Nodal analysis of constancy and fidelity of the East Flower Gardens reef fish.

sedentarius (reef butterflyfish), and *Bodianus pulchellus* (spotfin hogfish) were predominant at depths from 50 to 80 m (see Fig. 3 for abundance with depth of *C. enchrysura* and *Ch. sedentarius*). *Serranus annularis* (orangebacked bass), *Centropyge argi* (cherubfish), and *Liopropoma eukrines* (wrasse bass) represent species which were relatively restricted to this community. *Holocentrus rufus* (longjaw squirrelfish) and *Mycteroperca* spp. (groupers) were most common near partly drowned reefs within this zone. The zone extends deeper at the WFG (approx. 88 m) than at the EFG (approx. 82 m) due to deeper surrounding bottom depth at the WFG and therefore deeper nepheloid layer. Seventy-seven species were observed from 45 to 85 m with only 17% (13) of these species restricted to depths below 45 m (Appendix Table 1).

In comparing all fish assemblages resolved at the Flower Garden banks the algal-sponge zone assemblage had the highest Shannon-Weiner diversity (Table 2). Although the number of species was greatest for this zone, the evenness component of diversity was low (0.473) due to the dominance of a few species.

Table 2. Community diversity indices for the reef fish assemblages identified by cluster analysis at the Flower Garden banks (based on submersible observations only)

	Depth range (m)	Species (no.)	H'	J'	Survey time (h)	Area (km²)
WFG	<45	28	1.460	0.438	3.34	1.07
WFG	45–85	45	1.660	0.436	14.40	17.69
WFG	>85	20	1.310	0.437	5.39	56.14
EFG	<45	39	1.761	0.481	22.54	5.74
EFG	45–85	51	1.858	0.473	36.16	22.40
EFG	>85	12	1.309	0.527	8.75	21.13

A major division in the clustering of depth groups occurs between 80 and 90 m at both Flower Garden banks (Fig. 4). Few species are represented in the drowned reef zone (depth groups 4, 5, and 6) extending from 85 to 130 m. Species group VI is most characteristic of this zone with the *Holanthias martinicensis* (roughtongue bass) and *Serranus phoebe* (tattler) found in greatest abundance here (Fig. 5). *Lutjanus* spp. (snappers) were common in the shallower portion of the zone from 85 to 90 m (Fig. 3). *Priacanthus arenatus* (bigeye) along with several soft bottom related taxa such as Bothidae, Triglidae, Synodontidae, and Scorpaenidae were more commonly encountered below 85 m where carbonate rubble facies give way to terriginous sediments.

H' decreased in the deep water assemblage compared to shallower zones, and there was a sharp decrease in number of taxa with increasing depth (Table 2). Only 35 species were observed below 85 m with 14% (5) of these restricted to the drowned reef zone (Appendix Table 1).

Comparisons among Bank Groups.—Cluster analysis of the reef fish data from all banks resolved the banks into their previously recognized geological groupings (Fig. 7). This suggests that bank structure, depth, and location are significant determiners of the reef fish community structure. Results are compared within the following bank groups: shelf-edge, mid-shelf, and south Texas fishing banks.

Mean H' values for the shelf-edge, mid-shelf, and south Texas fishing banks were estimated at 1.531 (excluding the Flower Garden banks), 1.589, and 1.446, respectively. The Kruskal-Wallis test ($P < 0.05$) showed no significant differences among the Shannon-Wiener diversity means for the various bank groups. Nor were significant differences (Kruskal-Wallis test, $P < 0.05$) found between the mean evenness values for the bank groups (Table 3).

SHELF-EDGE BANKS. Ninety-five species of reef fish were observed on the shelf-edge banks excluding the Flower Garden banks. Seventy-three percent (69) of the species observed on these banks were classified as primary reef fish (Appendix Table 1). In the water column over these banks *Paranthias furcifer* was common along with the more pelagic species such as *Caranx crysos* (blue runner), *Seriola* spp. (amberjacks) and small scombrids. *Bodianus rufus, Holacanthus tricolor* (rock beauty), *Holocentrus rufus, Liopropoma eukrines,* and *Pseudupeneus maculatus* (spotted goatfish) were frequently encountered near reef outcrops. *Chromis enchrysura* and *Chaetodon sedentarius* were prevalent from 60 to 90 m with *Holanthias martinicensis* and *Serranus phoebe* more common from 88 to 110 m. The lutjanids, *Lutjanus campechanus* (red snapper) and *Rhomboplites aurorubens* (vermilion snapper) were observed, but in relatively low numbers.

Several species were found exclusively on the shelf-edge banks (including the

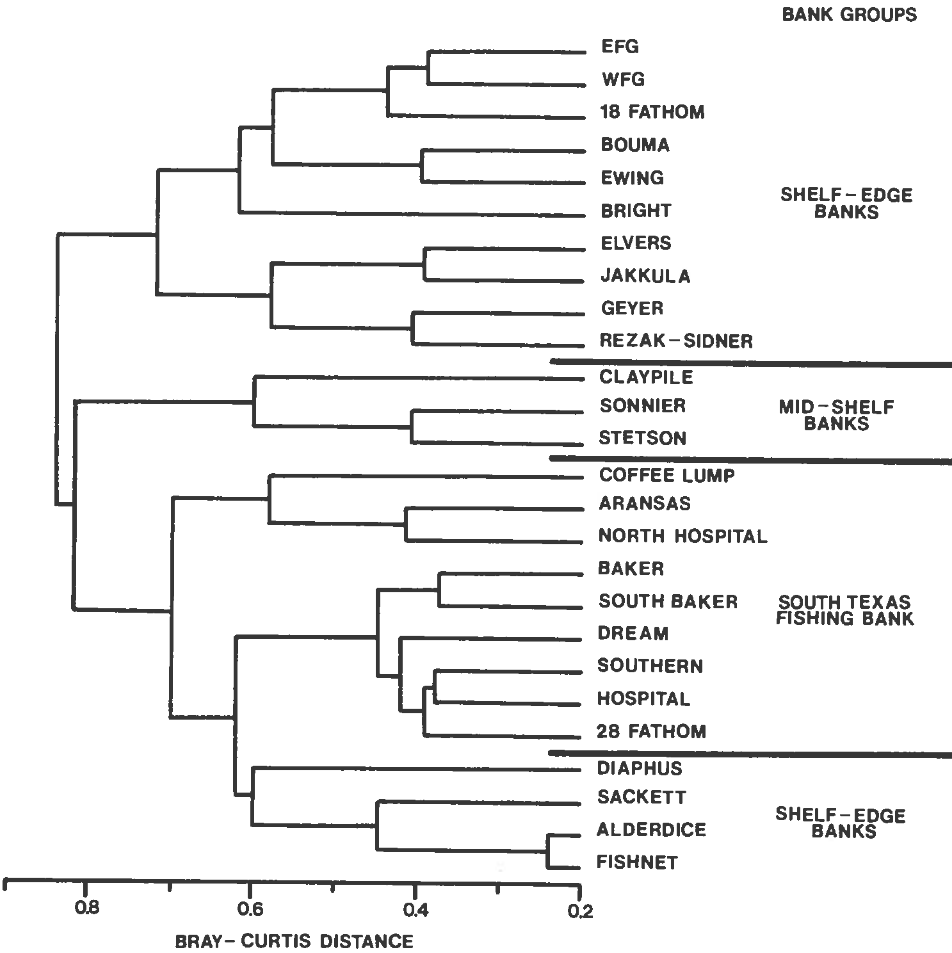

Figure 7. Cluster analysis of all banks based on submersible reef fish observations.

Flower Garden banks): *Amblycirrhitus pinos* (redspotted hawkfish), longsnout butterflyfish (*Chaetodon aculeatus*), *Chaetodon aya* (bank butterflyfish), *Chaetodon striatus* (banded butterflyfish), *Epinephelus inermis* (marbled grouper), *Haemulon striatum* (striped grunt), and *Sparisoma atomarium* (greenblotch parrotfish). *Xanthichthys ringens* (sargassum triggerfish) and *Gonioplectrus hispanus* (Spanish flag) were exceptionally common on the shelf-edge banks compared to the other banks sampled.

MID-SHELF BANKS. The reef fish community is quite diverse on the mid-shelf banks with 76 species (51 primary reef species) observed from the submersible or by SCUBA divers at only three locations sampled (Appendix Table 1). Pomacanthids such as *Holacanthus bermudensis* (blue angelfish), *Holacanthus ciliaris* (queen angelfish), and *Pomacanthus paru* (French angelfish) as well as labrids, notably *Halichoeres bivittatus* (slippery dick) and *T. bifasciatum*, were prevalent on these banks. *Clepticus parrai* and *P. furcifer* were common in midwater above most reef crests. *Chaetodon sedentarius* was common but *C. enchrysura* was in lower abundance than observed on other banks. *Chromis scotti* (purple reeffish)

Table 3. Mean community diversity indices, Shannon-Wiener diversity (H') and Pielou's evenness (J') for each of the hard bank groups

		H'		J'	
Bank group	N	$\bar{x}$	SD	$\bar{x}$	SD
Mid-shelf Banks	3	1.589	0.279	0.450	0.053
South Texas Fishing Banks	7	1.446	0.090	0.493	0.039
Shelf-edge Banks					
Including the Flower Gardens	15	1.598	0.216	0.452	0.039
Excluding the Flower Gardens	13	1.531	0.120	0.450	0.040
Kruskal-Wallis Test ($P = 0.05$)		n.s.		n.s.	

was particularly abundant at Sonnier bank, in the absence of *C. enchrysura*. Both *L. campechanus* and *R. aurorubens* were common on these banks, but *Mycteroperca* spp. were less so. The most common serranid observed on the mid-shelf banks was *E. adscensionis*. *Haemulon aurolineatum* (tomtate) was the most abundant grunt on the mid-shelf banks, replacing *Haemulon melanurum* (cottonwick) which is more common on the shelf-edge banks.

Three species occurred in especially high abundance on mid-shelf banks, *Chromis scotti*, *Ioglossus calliurus* (blue goby), and *Rypticus maculatus* (whitespotted soapfish).

South Texas Fishing Banks. The south Texas fishing banks are well known for their abundances of snappers (*Lutjanus* spp. and *Rhomboplites aurorubens*) and groupers (*Mycteroperca* spp.) (Fable, 1980). These species were also abundantly observed during our study. Schools of *Seriola dumerili* and *S. rivoliana*, *Caranx crysos*, and *Sphyraena barracuda* (barracuda) were common over most south Texas fishing banks. Both *Chromis enchrysura* and *Chaetodon sedentarius* were abundant on high relief areas of the bank crests, where most of the reef fish aggregated.

The overall number of reef fish (66 species visually observed) is low for these banks and the proportion of primary reef species (64%) was the lowest among the bank groups (Appendix Table 1). Coral-reef fish taxa were especially limited. The more frequently observed species included *Bodianus pulchellus*, *Liopropoma eukrines*, and *Priacanthus arenatus* (see Appendix Table 1 for other species) which, on the shelf-edge banks, typify the deeper algal-sponge zone. *Holanthias martinicensis* and *S. phoebe* were frequently observed on the south Texas fishing banks but at comparatively shallow depths (61 to 80 m).

Discussion

Flower Garden Banks.—Three distinct reef fish assemblages were resolved by cluster analysis at the Flower Garden banks: the coral reef, algal-sponge, and drowned reef assemblages. These assemblages closely parallel the known epifaunal communities and are apparently persistent features of the Flower Garden banks insofar as they were observed to be present over the 10 year time frame of this project.

The coral reef zone of the Flower Garden banks, less than 45 m depth, is similar in species composition to the outer reef slope communities of Caribbean reefs (Jones and Clark, 1981; Lukens, 1981). Substantially fewer primary reef fish species are found in this zone than on Caribbean reefs (84 vs. 253 primary reef fish species for one location in the Florida Keys) (Starck, 1968). Within our study

Table 4. Transient species in the northwestern Gulf based on their abundance and frequency of occurrence

Abudefduf saxatilis	*	*Holocentrus vexillarius*	
Acanthurus chirurgus		*Hypoplectrus unicolor*	?
Aluterus monoceros		*Lachnolaimus maximus*	
Anisotremus virginicus		*Lutjanus analis*	
Calamus calamus	?	*Lutjanus apodus*	
Chaetodon capistratus		*Lutjanus jocu*	
Chaetodon striatus		*Mycteroperca tigris*	
Diodon hystrix	?	*Ocyurus chrysurus*	
Epinephelus fulvus		*Opistognathus aurifrons*	
Epinephelus striatus		*Pomacanthus arcuatus*	
Gymnothorax funebris	?	*Pomacentrus dorsopunicans*	
Gymnothorax vicinus		*Pomacentrus leucostictus*	?
Haemulon chrysargyreum	?	*Pomadasys crocro*	
Haemulon macrostomum	?	*Rypticus subbifrenatus*	
Haemulon parrai	?	*Scarus radians*	
Hemipteronotus novacula		*Urolophus jamaicensis*	

?—species for which records could not be substantiated.
*—has now established a permanent population on offshore oil platforms in this region.

area the coral reef zone has the greatest apparent species diversity of all fish assemblages on the hard banks, although the algal-sponge zone had the highest H′ statistic. The limited amount of submersible survey effort applied in the area above 40 m may account for the lower diversity measure of the coral reef zone.

Three major factors limit the number of reef fish occurring in the northwestern Gulf when compared to Caribbean reefs: (1) limited habitat diversity, (2) limited habitat area, and (3) distance from source populations. On Caribbean reefs, the close proximity of emergent reefs, patch reefs, sea grass beds, mangroves, as well as other habitats, favors the occurrence of a high number of fish species within a relatively small area. For example, while 14 species of grunts (*Haemulon* spp.) occur in the Caribbean, only 2 (*H. aurolineatum* and *H. melanurum*) are commonly associated with offshore reefs in the northwestern Gulf. We believe this is due to the lack of grass bed feeding areas near offshore reefs. The lack of habitat variety may also cause other common Caribbean species such as *Chaetodon striatus*, *Epinephelus fulvus* (coney), *Epinephelus striatus* (Nassau grouper), *Ocyurus chrysurus* (yellowtail snapper), and *Pomacanthus arcuatus* (gray angelfish), to be absent or transient in this region (Table 4). During some stage of their life history these species utilize habitats not found in the northwestern Gulf.

Limits on the number of reef fish species in the northwestern Gulf imposed by limited habitat area reflect the positive species-area relationship set forth in island biogeography theory (MacArthur and Wilson, 1967). Suitable habitat (hard substrate) makes up less than 3.0% of the region's continental shelf (Parker et al., 1983) and only 4 of the 26 banks surveyed possess coral reef communities favoring habitation by "coral reef" fish. The importance of the coral reef community as a fish habitat is demonstrated by the absence (or rarity) in the eastern Gulf of Mexico of several reef fish species which are found in the northwestern Gulf (Table 5). Although the eastern Gulf possesses ten times more hard-bottom area than the northwestern Gulf and is closer to source populations, it generally lacks substantial hermatypic coral development (except for the Florida Middle Grounds which is not a true coral reef). This absence of coral reef habitat may explain the absence of some reef fish species from the eastern Gulf.

The distance of the Flower Garden banks from potential source populations of reef fish in the southern Gulf and Caribbean (the closest known reef is off Cabo Rojo, Mexico, 700 km to the south as currents do not take a direct route across the Gulf) limits the number of species lacking extended planktonic larval stages, and possibly those with low densities in the ichthyoplankton (i.e., low dispersal capabilities) (MacArthur and Wilson, 1967). Once a species does colonize a hard bank it may be difficult for it to spread to other suitable habitats because the banks are isolated from one another by large expanses of inhospitable soft bottom.

Although hard data (such as studies of ichthyoplankton and sexual maturity of reef fish) are lacking, the large size of resident reef fish populations in the northwestern Gulf (many thousands of individuals of most species), their year-round occurrence, and observations of spawning behavior (pers. obs.) are evidence that the local populations are self perpetuating. The need for input from Caribbean sources is not apparent. There is however, input from other sources based on the periodic occurrence of some species observed in the northwestern Gulf. The infrequent occurrence of some of these species (e.g., *Ocyurus chrysurus* and *Pomacanthus arcuatus*) suggests a transient nature to their occurrence in the northwestern Gulf and that recruitment from outside the region is variable and unpredictable. This unpredictability is exemplified by *Hemipteronotus novacula* (pearly razorfish) which showed an unusually large pulse of recruits in 1962, but did not persist in the region (Darnell et al., 1983). Highly variable recruitment may account for the disappearance of some species from the hard banks and their continued absence from the region until favorable conditions replenish their populations (Hoese, 1965; Moore, 1975).

Most species were encountered year-round, and the similar species composition observed during quarterly SCUBA surveys indicate seasonal stability of the coral reef fish assemblage.

A second assemblage of reef fish utilize the extensive low relief area of the algal-sponge zone. Diminutive species such as *Chromis enchrysura, Chaetodon sedentarius, Centropyge argi,* and *Serranus annularis* use this area for foraging and shelter. Reef fish typical of the coral reef zone are predominantly found associated with higher relief areas in this zone known as partly drowned reefs. Deeper in the zone several species, such as *Bodianus pulchellus, Liopropoma eukrines, Mycteroperca* spp., and *Priacanthus arenatus,* replace typical coral reef species on partly drowned reefs. Although the total area of the algal-sponge zone is almost six times greater than the coral reef zone there were 24 fewer primary reef fish species observed. Diversity (H′), however, was greatest in the algal-sponge zone in part due to the edge effect (Odum, 1971), with species common to both the coral reef zone and algal-sponge zone being relatively abundant in the ecotone from 40 to 50 m.

There is a change in the algal-sponge zone in the type and abundance of food sources available to reef fish because with increasing depth there is a change from a hermatypic coral dominated community to a coralline algae dominated community. The change in species composition and reduction in number of reef fish species in this zone may be attributable to this change in food resources as well as to the low relief habitat.

The algal-sponge zone reef fish assemblage is similar in species composition to live bottom communities along the southeastern U.S. Atlantic coast, eastern Gulf of Mexico, and Caribbean. It is also very similar to the reef fish assemblage associated with the sponge community off Brazil (Collette and Rützler, 1977).

Several forms of species replacement are apparent in the algal-sponge zone in the northwestern Gulf. *Chromis enchrysura,* the most abundant algal-sponge zone species, occurs from North Carolina to mid-Brazil and throughout the tropics

Table 5. Primary reef fish which reside in the northwestern Gulf but are rare or absent from the eastern Gulf (based on data from Smith et al., 1975; Smith, 1976; Shipp and Hopkins, 1978; Hastings, 1979; Williams and Shipp, 1980; Bullock and Godcharles, 1982)

Species	Abundance in eastern Gulf	Species	Abundance in eastern Gulf
Acanthurus bahianus	Rare	*Holocentrus rufus*	Absent
Acanthurus coeruleus	Rare	*Lactophrys triqueter*	Absent
Amblycirrhitus pinos	Absent	*Melichthys niger*	Absent
Aulostomus maculatus	Rare	*Microspathodon chrysurus*	Absent
Balistes vetula	Rare	*Mulloidichthys martinicus*	Rare
Cantherhines macrocerus	Absent	*Mycteroperca interstitialis*	Rare
Cantherhines pullus	Absent	*Paranthias furcifer*	Rare
Canthidermis sufflamen	Absent	*Pomacanthus paru*	Rare
Centropyge argi	Rare	*Pomacentrus planifrons*	Rare
Chaetodon aculeatus	Absent	*Priacanthus arenatus*	Rare
Chromis cyanea	Rare	*Pseudupeneus maculatus*	Rare
Chromis multilineata	Absent	*Scarus taeniopterus*	Absent
Clepticus parrai	Absent	*Scarus vetula*	Absent
Diodon holocanthus	Absent	*Serranus annularis*	Absent
Epinephelus inermis	Rare	*Sparisoma aurofrenatum*	Rare
Haemulon melanurum	Absent	*Sparisoma viride*	Rare
Holacanthus tricolor	Rare	*Thalassoma bifasciatum*	Rare*
Holanthias martinicensis	Rare	*Xanthichthys ringens*	Absent
Holocentrus ascensionis	Rare*		

* Except at Florida Middle Grounds where common.

over live bottom habitats (Emery and Smith-Vaniz, 1982). It replaces shallow-water congeners, *C. cyanea* and *C. multilineata. Bodianus pulchellus* also replaces its shallow water congener *B. rufus* within this zone.

Both of the common Caribbean shallow water butterflyfishes, *Chaetodon capistratus* and *Ch. striatus* are transient members of the hard bank fauna while *Chaetodon sedentarius,* the second commonest species in algal-sponge zone and an indicator species of intermediate shelf reefs (24–59 m) off the southeastern U.S. Atlantic coast (Miller and Richards, 1979; Wenner, 1983) becomes numerically dominant over *Ch. ocellatus* below 40 m. Although *Ch. sedentarius* is found throughout the Caribbean (Böhlke and Chaplin, 1968; Randall, 1968) it seems to be most common on continental shelf live bottom habitat.

In the algal-sponge zone there is also evidence of the mixing of continental and insular faunas (Robins, 1971; Gilbert, 1972). Based on the fact that the hard banks are located on the continental shelf it might be assumed that the tropical fauna would be comprised of continental species, but both insular and continental species are common here. Both the insular grouper species *Mycteroperca interstitialis* and its continental congener replacement *M. phenax* are common in the northwestern Gulf as has been reported for the Campeche banks in the southern Gulf (Smith, 1971) while *Mycteroperca microlepis,* another continental species, abundant in the eastern Gulf and along the southeastern U.S. Atlantic coast is uncommon here (Smith, 1976; Grimes et al., 1982). Both insular *Holacanthus ciliaris* and continental *H. bermudensis* are common in the algal-sponge zone as in Florida (Feddern, 1968). *Serranus annularis* is an insularly distributed species commonly found along the U.S. continental shelf only off the Florida Keys and in the northwestern Gulf of Mexico, but is widely distributed in the Caribbean (Robins and Starck, 1961; Starck, 1968; this study). Also some continental species are abundant in this zone. *Liopropoma eukrines* is frequently found on continental shelf live bottoms in both the eastern and northwestern Gulf, but is rare in the Caribbean.

Reef fish species diversity becomes much lower within the nepheloid layer. Two small serranids, *Holanthias martinicensis* and *Serranus phoebe* dominate the fauna associated with hard substrates in the drowned reef zone (>80 m). *Holanthias martinicensis*, one of three relatively shallow-water anthiin species in the western Atlantic (Anderson and Heemstra, 1980), is most abundant from 80 to 90 m at the Flower Garden banks and has been observed down to 150 m. Although this apparently insular species is abundant in the Caribbean off Jamaica and Belize (Colin, 1974), it is replaced in dominance by the more continental *Anthias nicholsi* in the northeastern Gulf (Shipp and Hopkins, 1978) and along the southeastern U.S. Atlantic coast (Burgess et al., 1979).

Serranus phoebe seems to possess just the opposite distribution from *Holanthias martinicensis*, being common throughout the Gulf of Mexico and north to Cape Hatteras (Shipp and Hopkins, 1978; Wenner, 1983; this study), but absent in the Caribbean. Though Robins and Starck (1961) report *S. phoebe* from the Antilles, no individuals were observed by Colin (1974; 1976) off the Bahamas, Jamaica, or Belize.

Although *Chaetodon sedentarius* occurs down to 98 m, *Ch. aya* was the most abundant butterflyfish in the drowned reef zone. This species represents another continental form, being reported as more abundant than *Ch. sedentarius* in the eastern Gulf of Mexico (Shipp and Hopkins, 1978) and is likely to be the most abundant deepwater butterflyfish along the southeastern U.S. coast (Hubbs, 1963).

Several species (e.g., *Serranus phoebe* and *Priacanthus arenatus*) may compete effectively in the drowned reef zone by exploiting resources on soft bottom areas adjacent to drowned reefs. In these soft bottom areas other reef fish are apparently competitively excluded by typical continental shelf taxa such as triglids, bothids, synodontids, and scorpaenids.

The drowned reef zone lacks the epifaunal diversity of the two shallower zones apparently due to the effects of the nepheloid layer. This may explain the dominance of plankton feeding reef fish and may also limit reef fish species diversity on drowned reefs. Also, estimates of reef fish abundance on drowned reefs are much lower per unit area of habitat than for shallower zones. Since high relief areas are quite common below 70 m at the Flower Garden banks the lack of hard substrate cannot be considered a limiting factor for species diversity or abundance. Therefore, it is likely that limited epifaunal diversity results in lower reef fish diversity, while food limitations in this zone result in lower abundances.

Shelf-edge Banks.—A limited temperature range and reduced exposure to the nepheloid layer allow the shelf-edge banks to develop the greatest apparent reef fish species richness of any banks (other than the Flower Garden banks) in the northwestern Gulf of Mexico. These banks possess an algal-sponge zone community similar to that at the Flower Garden banks.

Below the nepheloid layer a typical drowned reef fish assemblage exists on these banks. The influence of the nepheloid layer on reef fish assemblages can be seen in the clustering of five shelf-edge banks closely with the south Texas fishing banks (Fig. 7). Diaphus and Sackett banks are the two banks closest to the turbid Mississippi and Atchafalaya River discharge. Alderdice, Coffee Lump, and Fishnet banks are in shallower surrounding depths on the continental shelf than other shelf-edge banks. These banks are considered transitional in biotic community development (Rezak et al., 1985). Coffee Lump and Fishnet banks were observed to be completely enveloped in the nepheloid layer during reef fish surveys. Coffee

Lump has relief and a crest depth similar to the south Texas fishing banks, to which it is most closely related based on reef fish cluster analysis.

Mid-shelf Banks.—The reef fish assemblage of the mid-shelf banks is surprisingly diverse even though it exists under relatively stressful hydrographic conditions (temperature minimum 16°C). These banks are somewhat removed from the buffering effect of the deeper Gulf waters and thus experience temperature fluctuations typical of the warm-temperate inner shelf. Reef fish diversity is attributable in part to the moderately high epibenthic diversity associated with the shallow reef crests of these mid-shelf banks. The water column is commonly turbid here due to storm mixing. This may exclude some insular species from the mid-shelf banks. Starck (1968) concluded that water turbidity prevented the establishment of some Bahamian fish in the Florida Keys. Further, Gilbert (1972) reported that some species which are rare in the Keys maintain permanent populations off Palm Beach, Florida, 100 km north of Miami, under less turbid water conditions. The common occurrence of *Chromis scotti, Haemulon aurolineatum, Ioglossus calliurus,* and *Pomacentrus variabilis,* characterizes the mid-shelf reef fish assemblage, which is quite similar to that reported for the Florida Middle Grounds (another location of a diverse tropical reef fish assemblage under stressful environmental conditions in the northeastern Gulf of Mexico) (Smith et al., 1975). These dominant species form a rather unique assemblage of northern tropical, continental reef fish which exhibit their greatest abundance in the Gulf of Mexico and southern Atlantic coast of the United States.

South Texas Fishing Banks.—The reef fish assemblage of these banks can best be described as a mixture of the algal-sponge and drowned reef zone species reported from the Flower Garden banks. Coral reef zone species are generally lacking. Reef fish diversity seems to be limited by two factors at the south Texas fishing banks: habitat area and epibenthic diversity. Habitat area is relatively small due to the lack of significant contemporary reef building activity as well as the small areal extent of these banks. Little hard substrate extends above the nepheloid layer and the crests of these banks are often inundated with turbid water. These conditions do not allow a diverse epibenthic community to develop, thus limiting reef fish food and habitat resource availability. Water remains above the tolerance limit (16°C) put forth by Miller and Richards (1979) for subtropical species.

Conclusions

Four reef fish assemblages were resolved in the northwestern Gulf of Mexico: coral reef, algal-sponge, drowned reef, and mid-shelf. Their spatial occurrence closely parallels that of distinct hard-bottom epibenthic communities from the region. Tropical communities in the northwestern Gulf are limited to the intermediate and outer continental shelf by winter cooling of inner shelf waters and high turbidity associated with the discharge of the Mississippi/Atchafalaya and other rivers.

The high reef fish diversity at the Flower Garden banks when compared to other banks in the region is due to the variety of habitats and stable, tropical environmental conditions. Fewer species occur in the northwestern Gulf of Mexico than in Caribbean waters because of (1) limited habitat diversity, (2) limited habitat area, and (3) isolation from source populations.

Isolation of the region alone cannot explain the absence of many species with protracted larval stages. This can probably best be explained by limited area and variety of habitat, and limited food resources. Limited food resources are more important with increasing depth insofar as fish populations in many deep water high relief areas were less abundant than the areas' apparent carrying capacity based on the availability of hard substratum alone.

Temperature is not considered a limiting factor to tropical community development on shelf-edge banks, though low winter temperatures may influence the mid-shelf and south Texas fishing banks fauna. Water turbidity and the temperature regime at mid-shelf banks allow a unique assemblage of shallow-water continental reef fish species to exist there.

Similarities in reef fish species composition on widely scattered banks within each bank group (shelf-edge, mid-shelf, and south Texas fishing banks) are due to similar crest depths and hydrographic conditions, which result in similar epibenthic communities.

Low reef fish species richness on any bank is associated with the presence of the nepheloid layer. Overall species richness of the region is limited much more by the nepheloid layer and limited habitat diversity than by water temperature.

The co-occurrence of several closely related species such as *Mycteroperca interstitialis/phenax, Holacanthus bermudensis/ciliaris* which have continental and insular ditributions, together with the community dominance of both continental (*Serranus phoebe*) and insular (*Holanthias martinicensis*) species indicate an ecotone between continental and insular tropical faunas within the northwestern Gulf.

Though the northwestern Gulf of Mexico may have an impoverished tropical reef fish fauna when compared to the Caribbean, it has a full complement of species for the type of habitat available for colonization.

Acknowledgments

Thanks go to those students who helped initially compile the submersible data: S. T. Viada, G. S. Boland, L. Kobuke, and R. Titgen. G. Wolff is thanked for his help in the clustering analysis and C. Combs for his help in database management. R. Darnell, J. McEachran, and S. Gittings provided comment and discussion on many ecological points and proofread the text. Comments from an anonymous reviewer helped clarify several important points. Figures were prepared by B. H. Bower-Dennis. This study was started by C. W. Cashman whose early compilation of the data made much easier the final analysis of the data. This report made up part of the senior author's thesis submitted as partial fulfillment of the Master's of Science degree in the Department of Oceanography, Texas A&M University. This research was supported by BLM Contracts AA550-CT6-18, AA550-CT7-15, AA551-CT8-35, and AA851-CT0-25.

Literature Cited

Anderson, W. D. and P. C. Heemstra. 1980. Two new species of western Atlantic *Anthias* (Pisces: Serranidae): redescription of *A. asperilinguis* and review of *Holanthias martinicensis*. Copeia 1980: 72–87.

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

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. EPA Report EPA-600/3-77-033. 114 pp.

Böhlke, J. E. and C. G. C. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood, Pennsylvania. 771 pp.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill Book Co., New York, New York. 475 pp.

Bright, T. J. 1977. Coral reefs, nepheloid layers, gas seeps and brine flows on hard banks in the northwestern Gulf of Mexico. Proc. 3rd Inter. Coral Reefs Symp. Miami 1: 39–46.

——— and C. W. Cashman. 1974. Fishes. Pages 339–409 *in* T. J. Bright and L. H. Pequegnat, eds. Biota of the West Flower Garden Bank. Gulf Publ. Co., Houston, Texas.

——— and L. H. Pequegnat (eds.). 1974. Biota of the West Flower Garden bank. Gulf Publ. Co., Houston, Texas. 435 pp.

———, G. P. Kraemer, G. A. Minnery and S. T. Viada. 1984. Hermatypes of the Flower Garden banks, northwestern Gulf of Mexico: comparison to other western Atlantic reefs. Bull. Mar. Sci. 34: 461–476.

———, J. W. Tunnell, L. H. Pequegnat, T. E. Burke, C. W. Cashman, D. A. Cropper, J. P. Ray, R. C. Tressler, J. Teerling and J. B. Wills. 1974. Biotic zonation on the West Flower Garden bank. *Idem.*, pp 3–54.

Bullock, L. H. and M. F. Godcharles. 1982. Range extensions of four sea basses (Pisces: Serranidae) from the eastern Gulf of Mexico with color notes on *Hemanthias leptus* (Ginsburg). Northeast Gulf Sci. 5: 53–56.

Burgess, G. H., G. W. Link and S. W. Ross. 1979. Additional marine fishes new or rare to Carolina waters. Northeast Gulf Sci. 3: 74–86.

Caldwell, D. K. 1959. Observations on tropical marine fishes from the northeastern Gulf of Mexico. Quart. J. Fla. Acad. Sci. 22: 69–74.

Camber, C. I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche banks. Fla. Bd. Cons. Mar. Res. Lab. Tech. Ser. No. 12. 64 pp.

Chittenden, M. E. and J. D. McEachran. 1976. Composition, ecology and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Texas A&M Univ. Sea Grant Publ. TAMU-SG-76-208. 104 pp.

Clifford, H. T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York, New York. 229 pp.

Colin, P. L. 1974. Observations and collections of deep-reef fishes off the coasts of Jamaica and British Honduras (Belize). Mar. Biol. 24: 29–38.

———. 1976. Observations of deep-reef fishes in the Tongue-of-the-Ocean, Bahamas. Bull. Mar. Sci. 26: 603–605.

Collette, B. B. and K. Rützler. 1977. Reef fishes over sponge bottoms off the mouth of the Amazon River. Proc. 3rd Inter. Coral Reefs Symp. Miami 1: 305–310.

Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Co., Boston, Massachussetts. 509 pp.

Darnell, R. M., R. E. Defenbaugh and D. Moore. 1983. Northwestern Gulf shelf bio-atlas: a study of the distribution of demersal fishes and penaeid shrimp on soft bottoms of the continental shelf from the Rio Grande to the Mississippi River Delta. MMS OCS Office, Metairie, Louisiana. Open File Report No. 82-04. 438 pp.

Dawson, C. E. 1962. New records and notes on fishes from the northcentral Gulf of Mexico. Copeia 1962: 442–444.

Dennis, G. D. 1985. Tropical reef fish assemblages in the northwestern Gulf of Mexico. M.S. Thesis, Texas A&M Univ., College Station, Texas. 184 pp.

Emery, A. R and W. F. Smith-Vaniz. 1982. Geographic variation and redescription of the western Atlantic damselfish *Chromis enchrysura* Jordan and Gilbert (Pisces: Pomacentridae). Bull. Mar. Sci. 32: 151–165.

Fable, W. A. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and the vermillion snapper (*Rhomboplites aurorubens*) of the south Texas coast. Contri. Mar. Sci. 23: 115–121.

Feddern, H. A. 1968. Hybridization between the western Atlantic angelfishes, *Holacanthus isabelita* and *H. ciliaris*. Bull. Mar. Sci. 18: 351–382.

Field, J. G., K. R. Clarke and R. M. Warwick. 1982. A practical strategy for analyzing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8: 37–52.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge, England. 298 pp.

Gilbert, C. R. 1972. Characteristics of the western Atlantic reef-fish fauna. Quart. J. Fla. Acad. Sci. 35: 130–144.

Gladfelter, W. B., J. C. Ogden and E. H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61: 1156–1168.

Griffin, G. M. 1979. Evaluation of the effects of oil production platforms on the turbidity of Louisiana shelf waters. Rice Univ. Stud. 65(4/5): 159–179.

Grimes, C. B., C. S. Manooch and G. R. Huntsman. 1982. Reef and rock outcropping fishes of the outer continental shelf of North Carolina and South Carolina, and ecological notes on the red porgy and vermilion snapper. Bull. Mar. Sci. 32: 277–289.

Harrington, D. L. 1966. Oceanographic observations on the northwestern continental shelf of the Gulf of Mexico, 1963–1965. Contri. No. 329. NMFS Lab., Galveston, Texas. 25 pp.

Hastings, R. W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bull. Fla. Stat. Mus. Biol. Sci. 24: 1–124.

Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. Univ. Texas 3: 107–224.

Hoese, H. D. 1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Dissertation, Univ. Texas, Austin, Texas. 144 pp.

Hubbs, C. L. 1963. *Chaetodon aya* and related deep-living butterflyfishes: their variation, distribution, and synonymy. Bull. Mar. Sci. 13: 133–192.

Itzkowitz, M. 1974. A behavioural reconnaissance of some Jamaican reef fishes. Zool. J. Linn. Soc. 55: 87–118.

Jones, R. S. and M. Clark. 1981. Fishes. Pages 25–29 *in* S. C. Jameson, ed. Key Largo Coral Reef National Marine Sanctuary deep water resource survey. U.S. Dept. Commerce NOAA Tech. Rep. CZ/SP-1. 144 pp.

Lukens, R. R. 1981. Observations of deep-reef ichthyofauna from the Bahama and Cayman Islands, with notes on relative abundance and depth distribution. Gulf Res. Rept. 7: 79–81.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 pp.

Miller, G. C. and W. J. Richards. 1979. Reef fish habitat, faunal assemblages and factors determining distributions in the South Atlantic Bight. Proc. Gulf Carib. Fish. Inst. 32: 114–130.

Moore, R. H. 1975. Occurrence of tropical marine fishes at Pt. Aransas, Texas 1967–1973, related to sea surface temperature. Copeia 1975: 170–172.

Odum, E. P. 1971. Fundamentals of ecology. 3rd Edition. W.B. Saunders Co., Philadelphia, Pennsylvania. 574 pp.

Parker, R. O., D. R. Colby and T. D. Willis. 1983. Estimated amount of reef habitat on U.S. south Atlantic and Gulf of Mexico continental shelf. Bull. Mar. Sci. 33: 935–940.

Pielou, E. C. 1975. Ecological diversity. Wiley-Interscience, New York, New York. 165 pp.

Powles, H. and C. A. Barans. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42: 21–35.

Randall, J. E. 1968. Caribbean reef fishes. T.F.H. Publ., Jersey City, New Jersey. 318 pp.

Rezak, R., T. J. Bright and D. W. McGrail. 1985. Reefs and banks of the northwestern Gulf of Mexico: their geological, physical, and biological dynamics. John Wiley & Sons, New York, New York. 259 pp.

Robins, C. R. 1971. Distributional patterns of fishes from coastal and Gulf waters of the tropical western Atlantic. Pages 249–255 *in* Symposium on investigations and resources of the Caribbean Sea and adjacent regions. FAO Fish. Rep. 71.2.

——— and W. A. Starck. 1961. Material for a revision of *Serranus* and related fish genera. Proc. Acad. Nat. Sci. Phil. 113(11): 259–314.

———, R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. 4th Edition. Amer. Fish. Soc. Spec. Publ. No. 12. 174 pp.

Shipp, R. L. and T. S. Hopkins. 1978. Physical and biological observations of the northern rim of the Desoto Canyon made from a research submersible. Northeast Gulf Sci. 2: 113–121.

Smith, C. L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. Bull. Am. Mus. Nat. Hist. 146(2): 67–241.

Smith, G. B. 1976. Ecology and distribution of eastern Gulf of Mexico reef fishes. Fla. Dept. Nat. Res. Mar. Res. Publ. No. 19. 78 pp.

———, H. M. Austin, S. A. Bortone, R. W. Hastings and L. H. Ogren. 1975. Fishes of the Florida Middle Ground with comments on ecology and zoogeography. Fla. Dept. Nat. Res. Mar. Res. Publ. No. 9. 14 pp.

Sonnier, F., H. D. Hoese, and J. Teerling. 1976. Observations on the offshore reef and platform fish fauna of Louisiana. Copeia 1976: 105–111.

Starck, W. A. 1968. A list of the fishes of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. Undersea Biol. 1: 4–40.

Wenner, C. A. 1983. Species associations and day-night variability of trawl-caught fishes from the inshore sponge-coral habitat South Atlantic Bight. U.S. Fish. Bull. 81: 537–552.

Williams, J. T. and R. L. Shipp. 1980. Observations on fishes unrecorded or rarely encountered in the northeastern Gulf of Mexico. Northeast Gulf Sci. 4: 17–27.

DATE ACCEPTED: April 26, 1988.

ADDRESS: *Department of Oceanography, Texas A&M University, College Station, Texas 77843;* PRESENT ADDRESS: *(G.D.D.) Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00709-5000.*

Appendix Table 1. List of visually observed fish species from the northwestern Gulf of Mexico hard banks based on submersible, SCUBA diver, and photographic records. Observations at Flower Garden banks divided among the three assemblages by depth in meters. Primary reef fishes are denoted in final category. A—abundant; C—common; F—frequent; O—occasional; R—rare; X—present; P—primary

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Orectolobidae										
Ginglymostoma cirratum	O			R				X		
Rhincodontidae										
Rhincodon typus	X						X			
Carcharhinidae	F								O	
Carcharhinus falciformis	X			O				X	X	
Carcharhinus leucas	X									
Galeocerdo cuvieri	R			R						
Mustelus norrisi									R	
Rhizoprionodon terraenovae								R	X	
Sphyrnidae										
Sphyrna cf. *lewini*	O							R		
Squatinidae										
Squatina dumerili			R							
Pristidae										
Pristis sp.	R									
Dasyatidae										
Dasyatis americana				R				X	R	
Myliobatidae										
Aetobatus narinari	O									
Mobulidae										
Manta birostris	O			O						
Muraenidae										
Gymnothorax moringa	O	O		O	R		O	O	R	P

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Ophichthidae										
Myrichthys acuminatus		X								P
Ophichthus rex			O			O	O	O	O	
Synodontidae	R	O	O	R	O	O				
Synodus intermedius	X				X		O		R	
Synodus synodus								X		P
Antennariidae										
Antennarius radiosus				X						
Ogcocephalidae			R			O				
Holocentridae										
Holocentrus spp.*	O	F	O	O	F	O	F	F	O	
H. ascensionis	X	X			X		X	X	X	P
H. marianus		X					X			P
H. poco	X									P
H. rufus		X		X	X		X	X	X	P
H. vexillarius	X			X						P
Myripristis jacobus	R			R			R	O		P
Plectrypops retrospinis									R	P
Aulostomidae										
Aulostomus maculatus	O			O					R	
Centriscidae										
Macrorhamphosus scolopax							O			
Serranidae										
Epinephelus adscensionis	O	O		O	O			F		P
E. cruentatus	O	X		X				O		P
E. flavolimbatus							O			
E. fulvus	R			R						P
E. guttatus	R			X			X			P
E. inermis	O	O	R	R	O		O			P
E. niveatus							O			

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
E. striatus							R			P
Gonioplectrus hispanus						R	O	R		P
Hemanthias spp.							X		X	P
Holanthias martinicensis		O	C		C	A	C		F	P
Liopropoma eukrines	O	F	R	O	O		O	O	O	P
Mycteroperca spp.†	O	F	O	O	F	F	F	O	C	P
M. bonaci	X			X					X	P
M. interstitialis	X	X			X		X	X		P
M. phenax	X	X			X		X	X	X	P
M. tigris	R			R			R	R		P
M. venenosa	X	R					R			P
Paranthias furcifer	C	F		A	C		C	C	O	P
Serranus annularis	O	F		O	F		O		R	P
S. phoebe		F	F		O	F	F	O	F	P
Grammistidae										
Rypticus maculatus								O		P
Priacanthidae										
Priacanthus arenatus	O	F	O		F	O	O	O	F	P
Pristigenys alta							X		X	P
Apogonidae	O		O	O	O		O	O	O	P
Apogon aurolineatus							X			P
A. maculatus		O					X	X	X	P
A. pseudomaculatus							X			P
Malacanthidae										
Caulolatilus sp.			R				O			
Malacanthus plumieri	O	O		O	O		O		O	P
Pomatomidae										
Pomatomus saltatrix								R		
Echeneidae									O	

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Carangidae										
Caranx spp.	X	X		F	O	O				
C. crysos	O	O		O	O		F	O	F	
C. hippos	R								X	
C. latus	O			O				R		
C. lugubris	R						X			
C. ruber	F	O		F	O		X			P
Elagatis bipinnulata	O	X		R					R	
Selene setapinnis									X	
S. vomer								R		
Seriola dumerili	O	F		O	F	O	F	O	C	
S. rivoliana	X	X		X	X		X	X	X	
Lutjanidae										
Lutjanus apodus								R	R	P
L. campechanus	O	F	F		F		F	C	C	
L. griseus	O						X			
L. jocu				X			X			P
L. synagris								X	X	
Ocyurus chrysurus				R						P
Rhomboplites aurorubens		O			C	F	F	C	F	P
Haemulidae										
Haemulon aurolineatum								R	R	P
H. melanurum	F	O	O	C	O		O	O	R	P
H. striatum							X			P
Orthopristis chrysoptera								O		
Inermiidae	X						X			P
Sparidae										
Calamus leucosteus		X						X		
Calamus nodosus	O	F		F	O		O	O	O	P
Diplodus sp.							X			
Lagodon rhomboides									R	
Pagrus pagrus		X	X		X	X	X	X		

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Sciaenidae										
Equetus lanceolatus		O		R	O	O	R		R	P
E. punctatus	X						R	R	R	P
E. umbrosus		R	O		R	O	O	O		
Mullidae										
Mulloidichthys martinicus	F			C	O		O	R		P
Pseudupeneus maculatus	F	O		F	O		F	F		P
Kyphosidae										
Kyphosus spp.‡	O			O						
Chaetodontidae										
Chaetodon aculeatus	O	O		F	O		O			P
C. aya		R			F	F	F		R	P
C. ocellatus	F	O			R		R	O	R	P
C. sedentarius	F	C	O	C	F	O	C	C	C	P
C. striatus	R									P
Pomacanthidae										
Centropyge argi	O	F	O	F	F		O			P
Holacanthus bermudensis	O	F		O	O	O	O	F	O	P
H. ciliaris	O	O		R	O		O	F	R	P
H. tricolor	O	O		O	O		F	R		P
Pomacanthus arcuatus	R									P
Pomacanthus paru	O	F		F	O	O	F			P
Pomacentridae										
Abudefduf saxatilis	R									P
Chromis cyanea	O			O			R			P
C. enchrysura	F	A	O	C	A	F	A	F	A	P
C. insolata	R			R			O	O	R	P
C. multilineata	C			A				O		P
C. scotti	R			X			O	O	O	P
Microspathodon chrysurus	O			O					O	P

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Pomacentrus partitus	F	O		O	R		O	O		P
P. planifrons	O			O						P
P. variabilis	O	R		O			O	O	R	P
Cirrhitidae										
Amblycirrhitus pinos	O	O		R			O	X		P
Labridae										
Bodianus pulchellus	O	F	O	O	F	F	F	O	F	P
B. rufus	F	O		F			R	O		P
Clepticus parrai	C	R		C			R	F		P
Halichoeres bivittatus				R	O		O	F	O	P
H. garnoti	R			R						P
H. maculipinna	X			X						P
H. radiatus	R	R		R					R	P
Hemipteronotus sp.	X								R	P
Thalassoma bifasciatum	F	R		O				F		P
Scaridae	O	R		O	O				R	
Scarus taeniopterus	R			X			R			P
Scarus vetula	X			X						P
Sparisoma atomarium		X					X		X	P
S. aurofrenatum	X	R		R	O		O			P
S. viride	O	R		O	R					P
Sphyraenidae										
Sphyraena barracuda	F	O		O			O	O	F	P
Opistognathidae										
Opistognathus aurifrons	O				X		O			P
Opistognathus cf. *lonchurus*		X					R			
Blenniidae										
Ophioblennius atlanticus	X			X			R	O		P

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Gobiidae										
Gobiosoma (*Elacatinus*) sp.	O	O		O	O		O	O	O	P
G. oceanops	X	X		X	X		O	X		P
Ioglossus calliurus		R					R	C	O	
Acanthuridae										
Acanthurus spp.§	O	R		O	R		O	O		
Acanthurus bahianus	O	R		O				X		P
A. chirurgus	R							X		P
A. coeruleus	O	R		O			R	O		P
Scombridae										
Euthynnus alletteratus				X		O	F	O	O	
Scomberomorus cavalla	X						O	O	O	
Scorpaenidae		O	F	R	O	O	O		R	
Triglidae		R	F		O		R			
Bothidae		O	O			O	O	R	R	
Balistidae										
Aluterus scriptus				X	X					P
Balistes capriscus		O			O		O	O	R	
B. vetula	O	R		O	O		O	O	O	P
Cantherhines macrocerus	R			R						P
C. pullus	R									P
Canthidermis sufflamen	F	O		F				R		
Melichthys niger	O			O			R			P
Xanthichthys ringens		R		R	O		O			P
Ostraciidae										
Lactophrys quadricornis		O		R	O		O	R		
L. triqueter	O			O						P
Tetraodontidae										
Canthigaster rostrata	O	O		O	R	O	O	O	R	P
Sphoeroides sp.	O						R		R	

Appendix Table 1. Continued

	EFG			WFG						
	<45	45–85	>85	<45	45–85	>85	Shelf-edge	Mid-shelf	STFB	Cat.
Diodontidae										
Diodon spp.‖	R	R	R		O					
Diodon holocanthus	X				X		O			P
No. of species	102	72	25	85	57	25	96	76	66	

* *Holocentrus* spp. includes *H. ascensionis* and *H. rufus*.
† *Mycteroperca* spp. includes *M. interstitialis* and *M. phenax*.
‡ *Kyphosus* spp. includes *K. incisor* and *K. sectatrix*.
§ *Acanthurus* spp. includes *A. bahianus* and *A. chirurgus*.
‖ *Diodon* spp. includes *D. holocanthus* and most likely some *D. hystrix* but not verified.