Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico

Michael A Dance, William F Patterson III, and Dustin T Addis

SEDAR45-RD-06

November 2015

BULLETIN OF MARINE SCIENCE. 87(3):301–324. 2011
http://dx.doi.org/10.5343/bms.2010.1040

FISH COMMUNITY AND TROPHIC STRUCTURE AT ARTIFICIAL REEF SITES IN THE NORTHEASTERN GULF OF MEXICO

Michael A Dance, William F Patterson III, and Dustin T Addis

ABSTRACT

Fish community and trophic structure were examined quarterly from fall 2004 through spring 2007 at 27 artificial reef sites located 15–20 mi south of Pensacola, Florida. Location of study sites was not reported to the public when reef modules were deployed in 2003, thus sites were presumed to be unfished. Community structure estimates were derived from video sampling that was performed with a micro remotely operated vehicle (ROV) equipped with a laser scale to estimate fish size. A total of 81,207 individuals from 77 different taxa was enumerated from video samples. Fish assemblages were dynamic in species richness, fish community structure, and trophic structure across time and by reef design. Total fish density, biomass, and species richness increased across time. Red snapper, *Lutjanus campechanus* (Poey, 1860), was by far the most abundant species (29% of individuals, 45% of total biomass), and its density and biomass increased over the course of the study. Differences in fish community structure were driven by sharp declines in grouper abundance and the proliferation of smaller fishes across time. Trophic structure was consistently dominated by invertivore/piscivores, while fluctuation in piscivore biomass and increased abundance of planktivores drove differences in trophic structure. Size distributions for many fishery species known to display low annual site fidelity were composed primarily of young, sub-legal individuals. Disappearance with increasing fish size was likely due to shifting ontogenetic habitat requirements or exposure to high regional fishing mortality for species that displayed low annual site fidelity to study sites.

Artificial reefs are commonly deployed in marine waters off the southeastern United States for a variety of purposes, including mitigating loss of hard-bottom habitat, enhancing fishery yields, enhancing production of reef-associated invertebrates and fishes, and creating opportunities for diving and fishing in nearshore environments (Stone et al. 1991, Spanier and Barshaw 1994, Baine 2001). Perhaps the most frequently stated objective of artificial reef construction is to recover overfished reef fish populations (Lindberg 1997). Increased catch rates and high fish densities at artificial reef sites have led some to perceive these structures as beneficial to fish stocks by providing increased hard bottom habitat to reef fishes (Minton and Heath 1998, Shipp and Bortone 2009). Recreational and commercial fishermen have been the biggest supporters of artificial reefs, and the idea that these structures provide beneficial habitat enhancement likely has been widely accepted because it is consistent with the conservation ethic of many fishermen (Lindberg 1997). This is of particular importance in the northern Gulf of Mexico (GOM) where many large reef fishes (e.g., gag *Mycteroperca microlepis*, red snapper *Lutjanus campechanus*, greater amberjack *Seriola dumerili*, and gray triggerfish *Balistes capriscus*) found at artificial reefs are estimated to either be fully exploited or overfished (Patterson and Cowan 2003).

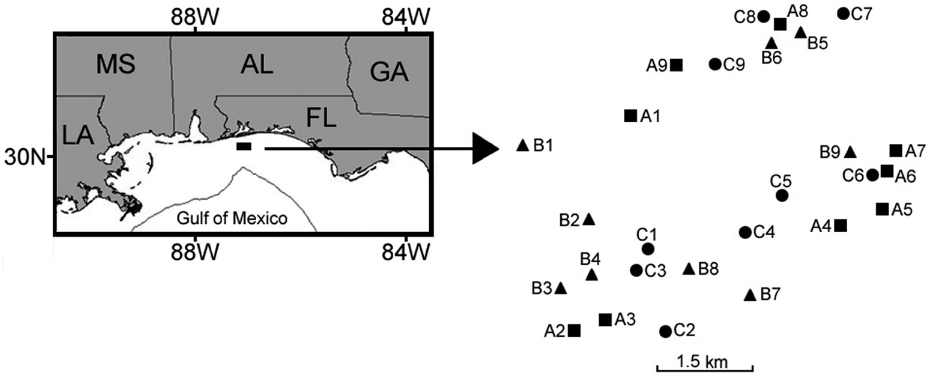

Figure 1. Map indicating the locations of study artificial reefs within the Escambia East Large Area Artificial Reef Site (black rectangle). Letters in reef names indicate A-, B-, or C-type reefs. The 200-m isobath is shown to indicate the edge of the continental shelf.

If reefs function ecologically to generate a net increase in fish production, then increased catch rates may be supported by enhanced productivity (Bohnsack 1989). Alternatively, if reefs function as a net sink of production, then high catch rates may encourage the continued mass deployment of artificial reefs, which in turn may push fishing mortality to unsustainable levels or exacerbate the already poor stock status of many species (Grossman et al. 1997). Historically, this dilemma has been called the attraction-production debate (Bohnsack and Sutherland 1985, Bohnsack 1989, Grossman et al. 1997). However, attraction and production are not mutually exclusive, but instead are two endpoints along a continuum (Bohnsack 1989, Lindberg 1997, Osenberg et al. 2002). A multitude of factors may influence where a given reef fish species will fall along this continuum, including fish behavior and site fidelity, fishing pressure, habitat availability, and recruitment limitation (Bohnsack 1989).

A unique opportunity to examine artificial reef function was created in 2003 in the northeastern GOM when the Florida Fish and Wildlife Conservation Commission (FWCC) deployed over 500 artificial reefs within four Large Area Artificial Reef Sites (LAARS) off northwest Florida. The coordinates of these sites were not reported to the public in hopes that the reefs would serve as no-harvest refugia for exploited reef fishes. In theory, enhanced production at these sites would allow them to act as net sources for local reef fish populations. While the purpose of establishing refugia sites was to mitigate against heavy fishing pressure on reef fishes, the hypothesis that they have a beneficial effect must be tested by examining community succession over time, as well as monitoring the size and population dynamics of fishes present on these reefs.

The objective of this research was to examine reef fish community and trophic structure among unpublished artificial reef sites of three different designs deployed within the Escambia East LAARS (EE-LAARS) off Pensacola, Florida (Fig. 1). Quarterly remotely operated vehicle (ROV) based video sampling was conducted over 3 yrs to examine seasonal and interannual shifts in community and trophic structure, as well as differences among reef types. The effects of sampling quarter and reef type on taxa- and trophic level-specific density, biomass, and size distribution estimates also were examined.

Methods

Reef Design and ROV Sampling.—Sampling occurred at a randomly chosen subset of 27 artificial reef sites located within the EE-LAARS off Pensacola, Florida, at depths ranging from 27 to 41 m (Fig. 1). Sites consisted of one of three different reef designs (Fig. 2), which was pre-determined based on FWC deployment of reefs in 2003. A-type reefs were pyramids that had concrete corners, mesh rebar sides, a height of 3.05 m, and a total reef volume of ~4.1 m^3 (Fig. 2A). B-type reefs consisted of paired three-sided, flat-topped concrete models with five triangular holes cut in each side and a smaller concrete module deployed in the center of each of the larger modules (Fig. 2B). Height of each module was 1.83 m and total reef volume was ~4.9 m^3. Lastly, C-type reefs consisted of paired 1.45-m tall dome-shaped concrete reefs that had a hollow center, a hole in the top, and numerous small cavities or passages into the reef center (Fig. 2C). Total volume for C-type reefs was the smallest of the three reef types at ~2.8 m^3.

Sampling was conducted quarterly from December 2004 through June 2007 (December, March, June, and September) with a VideoRay Pro3 micro ROV, which was equipped with a red laser scale (10 cm between lasers) to estimate fish length. The video feed from the ROV's 570-line camera was viewed on a 38-cm monitor and recorded with a digital videocassette recorder. At each site, the ROV first was flown to the seabed and then the point count method described by Patterson et al. (2009) was employed to video sample fishes. This method entailed conducting a series of four 30-s, 360° ROV spins to video sample fishes in a 15-m cylinder spanning the water column with the reef at the center of the bottom of the cylinder. Two spins were made just above the seabed on opposing sides of the reef at a distance of ~4 m from single or paired modules, a third spin 1 m above the reef, and a fourth spin ~10 m above the seafloor. Although B-type and C-type reefs were meant to be deployed such that modules were immediately adjacent to one another (Fig. 2B,C), modules of seven out of nine B-type reefs and two out of nine C-type reefs were > 8 m apart on the seabed. Therefore, modules of those sites were sampled independently.

Video Analysis.—In the laboratory, fishes from each video sample were identified to the lowest taxonomic level possible and then enumerated during video playback on a high resolution LCD monitor. Taxa-specific fish density was computed by dividing fish counts by the area of the sampling cylinder's base, which was 176.7 m^2. Fish density at B- and C-type reefs for which paired modules had to be sampled separately was computed by dividing the combined total count of the two cylinders by 353.4 $m^{2.}$

Fish length was estimated by multiplying the measured fork length (FL) of an individual fish in a digital image by the known distance between lasers (100 mm), and then dividing by the measured distance between the lasers in the image. Length was not estimated for any fish whose angular deviation from perpendicular to the camera, hence lasers, was evaluated to be > 15° based on results of a pool experiment reported by Patterson et al. (2009), from which measurement error was estimated to be < 5% for fish models viewed at angles < 20° from perpendicular and at distances < 5 m. Based on conditions observed in situ and results reported by Patterson et al. (2009), we estimated the mean bias of underestimating fish length with the ROV's laser scale was 3% with a standard deviation of 0.6%. Therefore, length estimates of all fishes measured with the laser scale were adjusted based on a random probability draw and normally distributed bias with mean equal to 3% and standard deviation equal to 0.6%. After correcting for measurement bias, fish length was converted to fish mass based on taxa-specific mass-length relationships reported in the literature (Nelson and Manooch 1982, Bohnsack and Harper 1988, Zhao et al. 1997). For taxa that were too small to be scaled with lasers, biomass estimates were computed by multiplying the total number of fishes observed by 80% of the maximum individual mass reported for a given taxon. Unidentified small fishes were assigned a mass of 1 g, which corresponds to the approximate mean mass at settlement for the predominant reef fishes observed in the study (Drass et al. 2000, Wells et al. 2008). Although

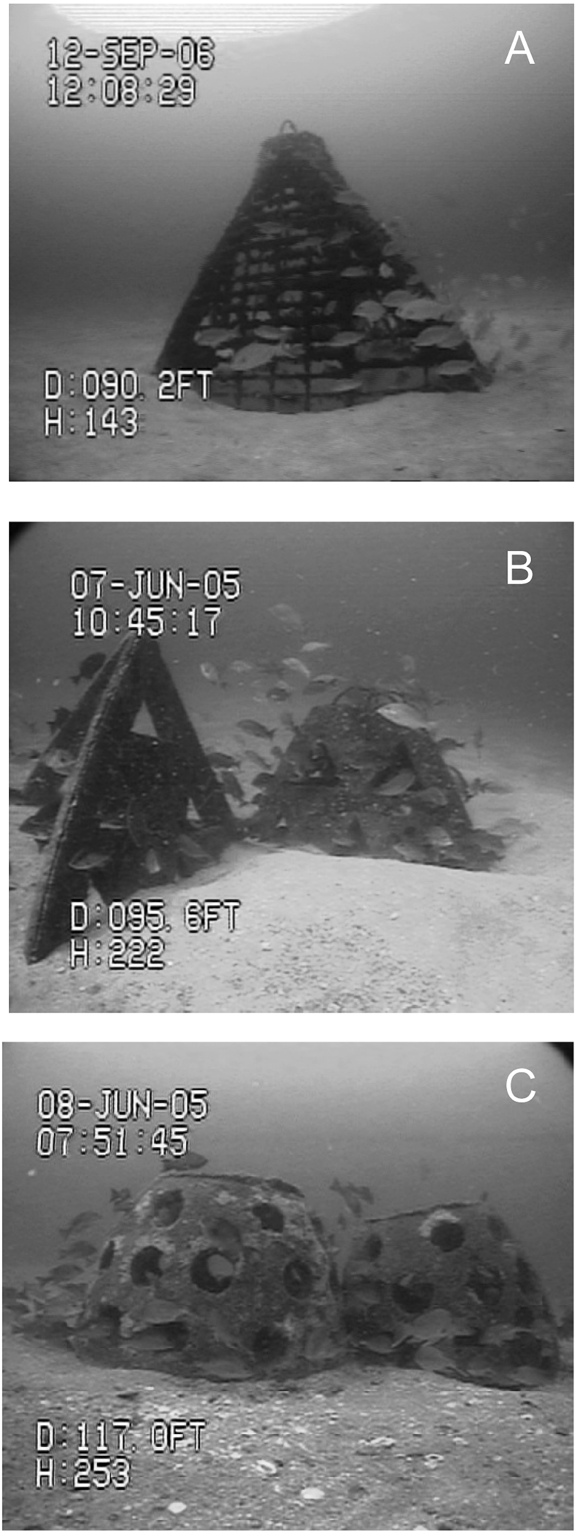

Figure 2. Digital images of (A) A-type, (B) B-type, and (C) C-type artificial reef study sites in the northeastern Gulf of Mexico.

these latter two methods may be somewhat arbitrary, taxa for which mass was assigned using either of them accounted for only 3.3% of the total fish biomass estimated at reef sites.

Data Analysis.—Two-way analysis of variance (ANOVA) models were computed to test the effects of sampling quarter and reef type, and their interaction, on species richness (number of fish taxa present), fish density (number 100 m^{-2}), and fish biomass (biomass 100 m^{-2}, SAS 2004). Normality was tested for each dependent variable with a Shapiro-Wilk's test and the assumption of homogeneity of variance was tested with a F-max test. Data were transformed when necessary to meet parametric assumptions.

The effects of sampling quarter and reef type were tested on reef fish community and trophic structure with analysis of similarity (ANOSIM) computed in Primer (Clarke 1993, Clark and Gorley 2001). First, taxa-specific fish density (number 100 m^{-2}) and biomass (biomass 100 m^{-2}) were square-root transformed to down-weight highly abundant taxa. Bray-Curtis similarity matrices were computed from the square-root transformed abundance data, and then two-factor (reef type × sampling quarter) ANOSIM models ($\alpha = 0.05$) were computed to test for differences in reef fish communities. For trophic structure analysis, fishes first were assigned to one of five trophic positions (planktivore, planktivore/invertivore, invertivore, invertivore/piscivore, and piscivore) based on literature reports of their predominant prey, as well as on unpublished stomach content and muscle stable isotope data from fishes sampled in the northern GOM. Then, ANOSIM models were computed as described above to test the effect of sampling quarter and reef type on trophic level-specific fish density and biomass.

Results

In total, 81,207 individuals from 77 different taxa were enumerated from video samples among the 3 yrs of sampling (Table 1), with 97.5% of individuals identified to species. The four most frequently encountered families in decreasing order of prevalence were Lutjanidae, Serranidae, Balistidae, and Carangidae, together accounting for 72% of the individuals by number and 89% of the total fish biomass. Red snapper was the dominant species among all samples, regardless of reef type or sampling quarter. Red snapper was observed in 97.6% of samples, constituted 29.9% of individuals observed, and its estimated biomass represented 45.1% of total fish biomass. Other large, exploited reef fishes observed frequently were gray triggerfish (81.1% of samples), scamp *Mycteroperca phenax* (61.5%), gag *Mycteroperca microlepis* (57.4%), red grouper *Epinephelus morio* (56.0%), greater amberjack *Seriola dumerili* (52.2%), and vermilion snapper *Rhomboplites aurorubens* (51.9%). However, no single species within that group constituted > 4% of total fish observed, although all ranked among the top 10 species in percent total biomass due to the relatively large size of individuals. Among smaller fishes, mackerel scad *Decapterus macarellus* (23.2%), tomtate *Haemulon aurolineatum* (8.9%), pinfish *Lagodon rhomboides* (6.1%), and round sardinella *Sardinella aurita* (3.4%) all ranked among the top 10 species in terms of the percent individuals observed, but only mackerel scad (4.6%) was among the top 10 with respect to percent total biomass. While small planktivores, such as mackerel scad, round sardinella, and blue runner *Caranx crysos* occurred infrequently at study sites (12.7% frequency of occurrence for mackerel scad was highest among these species), they often occurred in large numbers when present.

Species richness varied significantly with sampling quarter, as did fish density and biomass (ANOVA: $F_{10;255} > 2.67$, $P < 0.001$; Fig. 3). Only species richness was significantly different among reef types (ANOVA: $F_{2;255} = 6.31$, $P = 0.002$), and the interaction between reef type and sampling quarter was not significant in any model

Table 1. Fish taxa observed in video samples collected with a micro remotely operated vehicle at artificial reef study sites in the northeastern Gulf of Mexico. Family is given for groups in which at least two taxa were observed, with the exception of Haemulidae. For reef residency, R = reef resident, RA = seasonally reef-associated neritic pelagic species, S = demersal or benthic shelf species, and T = transient. For trophic position, H = herbivore, P = planktivore, I = invertivore, F = piscivore. For life stage, J = juvenile and A = adult. Multiple letters for trophic position indicate feeding at more than one trophic level. Multiple letters for life stage indicate more than one life stage present at study sites. Percent number is the taxon-specific percentage of total individuals observed among all sampling events. Percent mass is the taxon-specific percentage of total biomass estimated among all sampling events.

Taxon	Common name	Reef residency	Trophic position	Life stage	% frequency of occurrence	% number	% mass
Balistidae					81.9	3.78	7.12
Unknown Balistidae	triggerfish	R	I	A	1.0	0.01	0.01
Balistes capriscus Gmelin, 1789	gray triggerfish	R	I	A	81.1	3.77	7.11
Blennidae					22.2	0.72	0.02
Unknown Blennidae	blenny	R	PI	J, A	0.7	0.01	< 0.01
Hypleurochilus bermudensis Beebe and Tee-Van, 1933	barred blenny	R	I	A	0.3	< 0.01	< 0.01
Parablennius marmoreus (Poey, 1876)	seaweed blenny	R	I	A	21.3	0.71	0.02
Carangidae					72.2	27.83	13.26
Caranx crysos (Mitchill, 1815)	blue runner	T	PI	A	11.3	0.65	0.71
Caranx ruber (Bloch, 1793)	bar jack	T	IF	A	1.4	0.02	0.03
Decapterus macarellus (Cuvier, 1833)	mackerel scad	T	P	A	12.7	23.20	4.64
Elagatis bipinnulata (Quoy and Gaimard, 1825)	rainbow runner	T	IF	A	0.7	< 0.01	0.01
Hemicaranx amblyrhynchus (Cuvier, 1833)	bluntnose jack	T	IF	A	2.1	0.02	0.01
Seriola dumerili (Risso, 1810)	greater amberjack	RA	F	A	52.2	3.21	6.59
Seriola fasciata (Bloch, 1793)	lesser amberjack	RA	F	A	2.7	0.09	0.22
Seriola rivoliana Valenciennes, 1833	almaco jack	RA	F	A	36.4	0.63	0.99
Seriola zonata (Mitchill, 1815)	banded rudderfish	RA	F	A	1.0	0.01	0.06
Carcharhinidae					6.9	0.03	1.79
Carcharhinus limbatus (Müller and Henle, 1839)	blacktip shark	T	F	A	4.1	0.02	0.71
Carcharhinus plumbeus (Nardo, 1827)	sandbar shark	T	F	A	2.1	0.01	0.89
Carcharhinus spp.	requiem shark	T	F	A	0.7	< 0.01	0.19
Haemulidae					25.4	8.89	2.45
Haemulon aurolineatum Cuvier, 1830	tomtate	R	I	A	25.4	8.89	2.45

Table 1. Continued.

Taxon	Common name	Reef residency	Trophic position	Life stage	% frequency of occurrence	% number	% mass
Labridae					15.3	1.41	0.21
Halichoeres bivittatus (Bloch, 1791)	slippery dick	R	I	A	14.8	1.40	0.21
Xyrichtys novacula (Linnaeus, 1758)	pearly razorfish	R	I	A	1.0	0.01	< 0.01
Lutjanidae					99.0	36.71	54.49
Lutjanus campechanus (Poey, 1860)	red snapper	R	IF	A	97.3	29.92	45.05
Lutjanus griseus (Linnaeus, 1758)	gray snapper	R	IF	A	34	2.20	4.81
Lutjanus synagris (Linnaeus, 1758)	lane snapper	R	IF	A	32.6	0.64	0.61
Rhomboplites aurorubens (Cuvier, 1829)	vermilion snapper	R	PI	J, A	51.9	3.95	4.02
Monacanthidae					17.7	0.10	0.23
Aluterus heudeloti Hollard, 1855	dotterel filefish	R	I	A	0.7	< 0.01	0.01
Aluterus monoceros (Linnaeus, 1758)	unicorn filefish	R	I	A	8.9	0.05	0.12
Aluterus schoepfi (Walbaum, 1792)	orange filefish	R	I	A	4.8	0.03	0.06
Aluterus scriptus (Osbeck, 1765)	scrawled filefish	R	I	A	0.3	< 0.01	< 0.01
Monacanthus hispidus (Linnaeus, 1766)	planehead filefish	R	I	A	2.1	0.01	0.03
Monacanthus setifer (Bennett, 1831)	pygmy filefish	R	PI	A	0.7	0.01	0.01
Ostraciidae					2.1	0.01	0.01
Lactophrys quadricornis (Linnaeus, 1758)	scrawled cowfish	R	I	A	1.7	0.01	0.01
Lactophrys trigonus (Linnaeus, 1758)	buffalo trunkfish	R	I	A	0.3	< 0.01	< 0.01
Pomacentridae					10.1	0.50	0.04
Chromis enchrysurus Jordan and Gilbert, 1882	yellowtail reeffish	R	P	J, A	7.2	0.48	0.04
Chromis spp.	damselfish	R	P	J, A	0.3	< 0.01	< 0.01
Stegastes leucostictus (Müller and Troschel, 1848)	beaugregory	R	P	J, A	0.3	< 0.01	< 0.01
Stegastes variabilis (Castelnau, 1855)	cocoa damselfish	R	P	J, A	1.7	0.01	< 0.01
Stegastes spp.	damselfish	R	P	J, A	0.3	0.01	< 0.01

Table 1. Continued.

Taxon	Common name	Reef residency	Trophic position	Life stage	% frequency of occurrence	% number	% mass
Sciaenidae					12.8	0.18	0.13
Equetus acuminatus (Bloch and Schneider, 1801)	high-hat	R	I	A	2.1	< 0.01	< 0.01
Equetus iwamotoi (Miller and Woods, 1988)	blackbar drum	R	I	A	0.3	0.01	0.01
Equetus lanceolatus (Linnaeus, 1758)	jackknife fish	R	I	A	9.6	0.13	0.06
Equetus spp.	reef drum	R	I	A	0.3	< 0.01	< 0.01
Pareques umbrosus (Jordan and Eigenmann, 1889)	cubbyu	R	I	A	6.2	0.04	0.01
Sciaenops ocellatus (Linnaeus, 1766)	red drum	T	IF	A	0.3	< 0.01	0.05
Serranidae					97.9	4.47	14.27
Centropristis ocyurus (Jordan and Evermann, 1887)	bank seabass	S	I	A	17.9	1.17	0.82
Diplectrum formosum (Linnaeus, 1766)	sand perch	S	IF	A	6.5	0.16	0.08
Epinephelus drummondhayi Good and Bean, 1878	speckled hind	R	IF	J	0.7	< 0.01	< 0.01
Epinephelus morio (Valenciennes, 1828)	red grouper	R	IF	A	56.0	0.58	4.36
Epinephelus nigritus (Holbrook, 1855)	warsaw grouper	R	IF	J	1.4	0.01	< 0.01
Epinephelus niveatus (Valenciennes, 1828)	snowy grouper	R	IF	J	1.4	0.29	0.05
Hypoplectrus spp.	hamlet	R	IF	A	0.7	< 0.01	< 0.01
Mycteroperca microlepis (Good and Bean, 1879)	gag	R	F	A	57.4	1.14	7.31
Mycteroperca phenax Jordan and Swain, 1884	scamp	R	F	A	61.5	0.70	1.54
Rypticus maculates Holbrook, 1855	whitespotted soapfish	R	I	A	52.9	0.47	0.11
Sparidae					36.8	6.92	2.47
Calamus leucosteus Jordan and Gilbert, 1885	whitebone porgy	S	I	A	0.7	< 0.01	0.01
Calamus nodosus Randall and Caldwell, 1966	knobbed porgy	S	I	A	2.7	< 0.01	0.01
Calamus spp.	porgy	S	I	A	1.4	0.01	0.02
Lagodon rhomboids (Linnaeus, 1766)	pinfish	T	I	A	3.4	6.14	1.86
Pagrus pagrus (Linnaeus, 1758)	red porgy	R	I	A	33.7	0.76	0.57
Stenotomus caprinus Jordan and Gilbert, 1882	longspine porgy	S	I	A	0.7	0.01	< 0.01

Table 1. Continued.

Taxon	Common name	Reef residency	Trophic position	Life stage	% frequency of occurrence	% number	% mass
Other taxa							
Apogon pseudomaculatus Longley, 1932	twospot cardinalfish	R	P	J, A	5.8	0.65	0.01
Chaetodipterus faber (Broussonet, 1782)	Atlantic spadefish	R	I	A	9.6	1.73	0.48
Chaetodon ocellatus Bloch, 1787	spotfin butterflyfish	R	I	A	1.0	< 0.01	< 0.01
Chilomycterus atinga (Linnaeus, 1758)	spotted burrfish	R	I	A	2.7	0.01	0.03
Dasyatis Americana Hildebrand and Schroeder, 1928	southern stingray	S	IF	A	0.7	< 0.01	0.02
Echeneis naucrates Linnaeus, 1758	shark sucker	T	IF	A	2.4	0.02	0.04
Fistularia tabacaria Linnaeus, 1758	cornetfish	R	F	A	1.4	0.01	0.03
Ginglymostoma cirratum (Bonnaterre, 1788)	nurse shark	S	IF	A	3.1	0.01	1.24
Holacanthus bermudensis Goode, 1876	blue angelfish	R	I	A	20.3	0.08	0.16
Hyperoglyphe perciformis (Mitchill, 1818)	barrelfish	T	PI	A	0.3	< 0.01	< 0.01
Kyphosus spectator (Linnaeus, 1758)	Bermuda chub	R	HI	A	0.3	< 0.01	< 0.01
Paralichthys albigutta Jordan and Gilbert, 1882	gulf flounder	S	IF	A	1.4	< 0.01	0.01
Priacanthus arenatus Cuvier, 1829	Atlantic bigeye	R	PI	A	1.0	0.01	0.01
Rachycentron canadum (Linnaeus, 1766)	cobia	T	F	A	0.7	< 0.01	0.18
Sardinella aurita Valenciennes, 1847	round sardinella	T	P	A	0.7	3.39	0.73
Scomberomorus cavalla (Cuvier, 1829)	king mackerel	T	F	A	3.8	0.02	0.17
Sphyraena barracuda (Edwards, 1771)	greater barracuda	RA	F	A	3.4	0.01	0.16
Unknown small fishes	Unk. small fishes				14.4	2.44	0.27

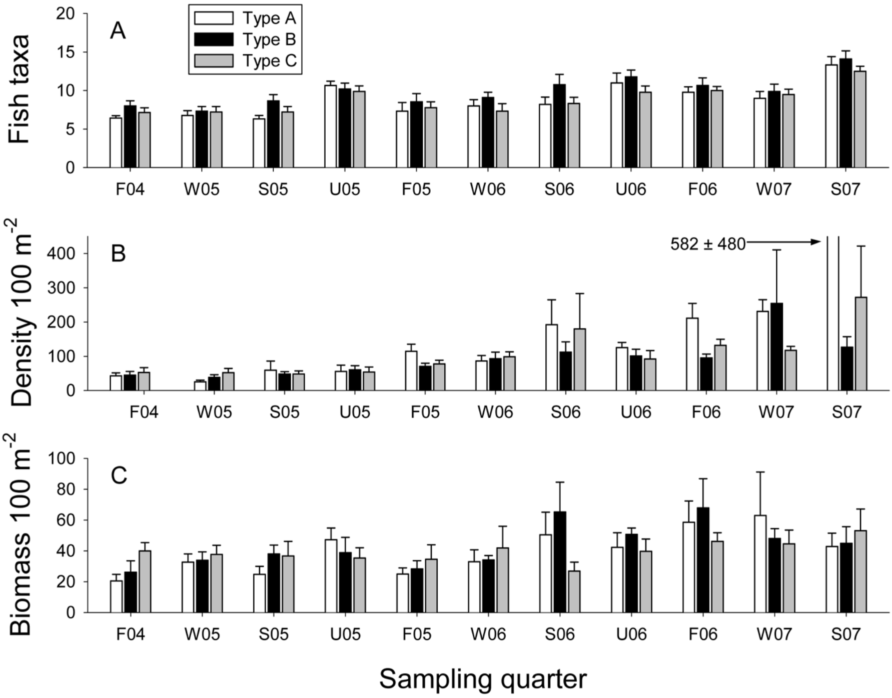

Figure 3. Mean + SE (A) number of fish taxa, (B) fish density, (C) fish biomass, estimated from video samples of fish communities associated with artificial reef sites in the northeastern Gulf of Mexico. The legend in panel A applies to all panels. Abbreviations along *x*-axis: F = fall, W = winter, S = spring, and U = summer.

(ANOVA: $F_{20;255} = 1.05$, $P > 0.405$). In general, species diversity increased over the course of the study (Fig. 3A), with annual peaks in summer. B-type reefs (10.0 species) displayed greater mean diversity than either A-type or C-type reefs (8.8 species for both).

Fish community structure for both taxa-specific density and biomass was significantly different among sampling quarters and reef types (ANOSIM: $P < 0.001$). Trophic position-specific density and biomass were also significantly different for both sampling quarter and reef type (ANOSIM: $P < 0.001$). Fish communities in the first year consisted almost entirely of groupers, snappers, and gray triggerfish (Fig. 4). Fish assemblages in the second and third year of the study were characterized by a dramatic decline in grouper density, followed by increases in densities of mackerel scad, tomtate, and greater amberjack (Fig. 4). Small cryptic and juvenile fishes such as two-spot cardinalfish *Apogon pseudomaculatus*, slippery dick *Halichoeres bivittatus*, blenniids, and pomacentrids were also observed increasingly in the latter portion of the study. Pinfish and round sardinella were rare at study sites, but were observed in vast schools when present (Fig 4). Mackerel scad and tomtate were found in greater abundance at A-type reefs (Fig. 4). Two C-type reefs, C7 and C9, had increased densities of bank sea bass *Centropristis ocyurus*, sand perch *Diplectrum formosum*, and occasionally round sardinella beginning in the fall of 2005 (Fig. 4).

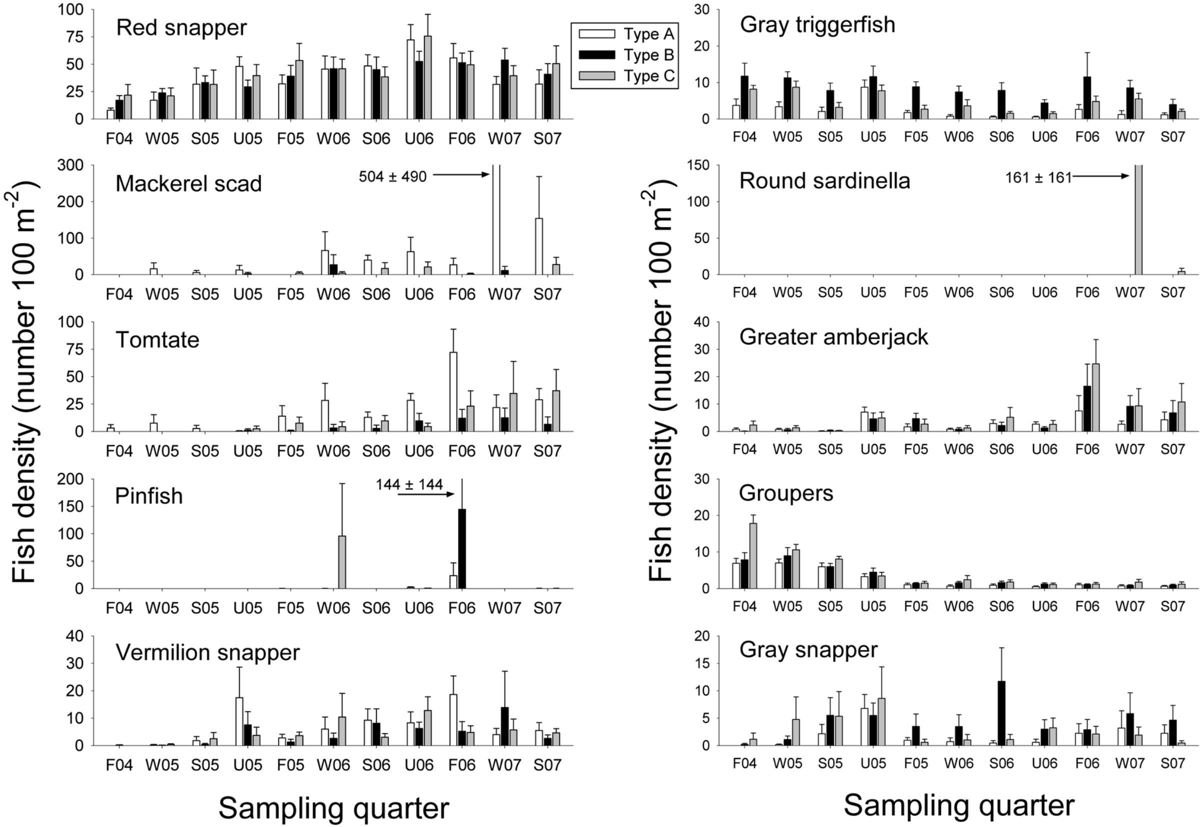

Figure 4. Mean + SE density of the 10 most abundant species estimated from video samples of fish communities associated with artificial reef sites in the northeastern Gulf of Mexico. Species presented in order of decreasing total abundance. Abbreviations along x-axis: F = fall, W = winter, S = spring, and U = summer. Legend applies to all panels.

Several trends were observed among fishes for which significant fisheries exist in the northern GOM. Red snapper density and biomass generally increased throughout the study, although there was a peak in summer 2006, and all three reef types tended to have high red snapper biomass (Fig. 4). Sharp declines in densities of gag, scamp, and red grouper likely drove an order of magnitude decline in grouper biomass in year one, which then remained at low levels (Fig. 4). Groupers tended to have the highest biomass on C-type reefs; gag, in particular, were often found in the central cavities of those modules. Density of gray triggerfish was variable among sampling quarters, but was highest on B-type reefs (Fig. 4). Greater amberjack and other *Seriola* spp. displayed the opposite pattern of groupers in that their density and biomass increased by an order of magnitude across the study (Fig. 4). Lastly, both vermilion snapper and gray snapper *Lutjanus griseus* displayed variable biomass among sampling quarters, although their biomass tended to increase from 2004 to 2007, particularly for vermilion snapper. Vermilion snapper densities were highest at A-type reefs, while gray snapper densities were greatest at B-type reefs (Fig. 4).

A-type reefs generally had the highest density of planktivorous fishes, and this trend became more pronounced over time (Fig. 5). The increasing yet variable presence of large schools of planktivores (e.g., mackerel scad, round sardinella, blue runner) at study sites was also largely responsible for the spike in fish density estimates in the latter part of the study (Fig. 3). Piscivore density and biomass decreased over the first year, and then increased in the last year of the study (Fig. 5). Planktivore/invertivores and invertivores generally increased across time in both density and biomass (Fig. 5). While planktivores displayed the highest densities of fishes overall, their small individual size translated to a biomass that was < 25% of that observed for piscivores and < 10% of that observed for invertivore/piscivores. Invertivore/piscivores density increased during the first year of the study and then remained high. (Fig. 5). Trophic assemblages were affected by the degree of reef residency among fishes present (Fig. 6). Reef residents were mostly invertivore/piscivore or invertivores (i.e., snappers, grunts, and triggerfish). Among transient or seasonally reef-associated pelagic species, planktivores were the most abundant numerically, while piscivores, such as *Seriola* spp. and sharks, were predominant by biomass.

Estimated fish length distributions provide important information about fishes present at study reefs beyond density and biomass estimates. Only 9% of red snapper were estimated to be > 406 mm TL, which was the recreational size limit for harvesting the species throughout the study (Fig. 7). Conversely, gray and vermilion snappers had the highest percentage of individuals above recreational size limits, with 72% of gray snapper above their size limit of 305 mm TL and 63% of vermilion snapper above their size limit of 255 mm TL (Fig. 7). Similarly, 38% of gray triggerfish were estimated to be above its recreational size limit of 305 mm FL (Fig. 7). *Seriola* spp. displayed a normal size distribution, with a mode at ~350 mm FL, which is well short of the recreational size limit for greater amberjack (762 mm FL), the predominant *Seriola* spp. observed (Fig. 7). Groupers had a broad size distribution, but this mostly reflects the species-specific variation in body size among gag, scamp, and red grouper.

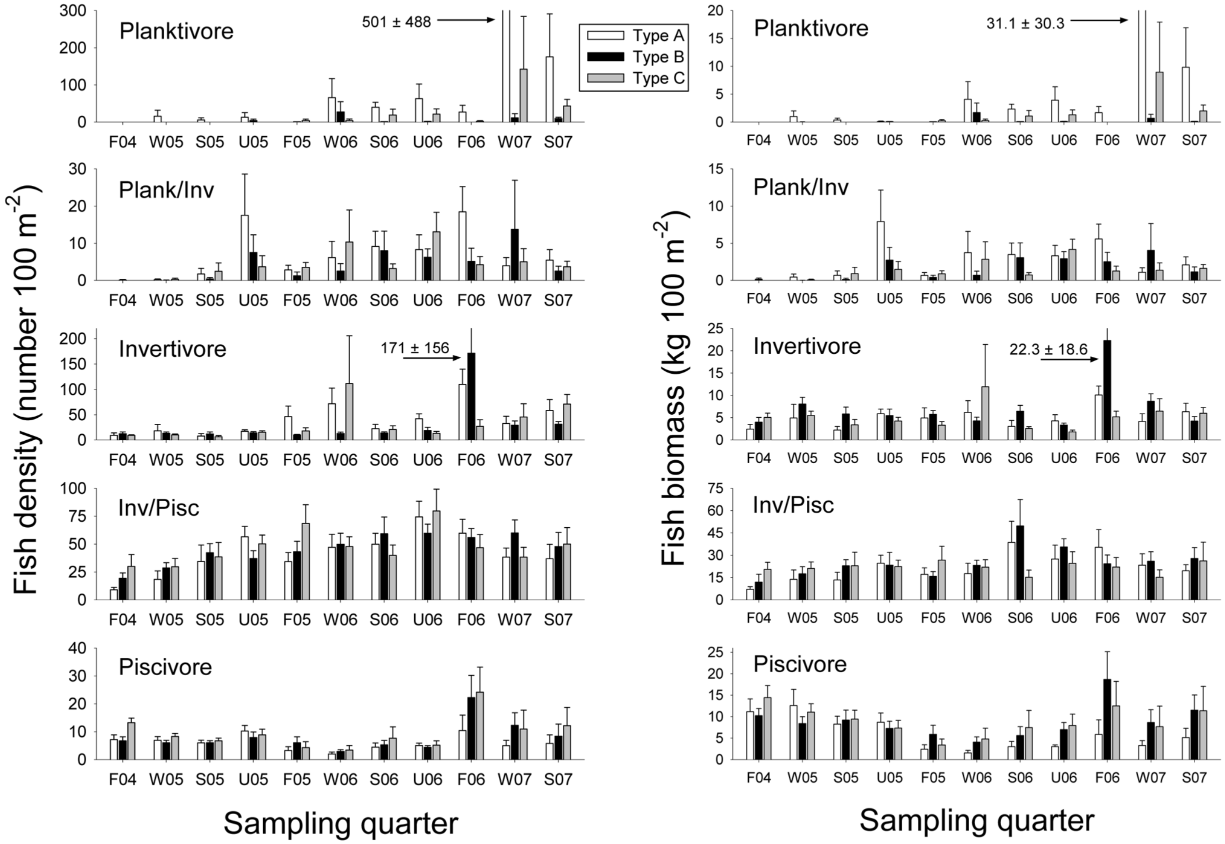

Figure 5. Mean + SE density and mean + SE biomass of different trophic groups observed within fish communities associated with artificial reef study sites in the northeastern Gulf of Mexico. Plank/Inv refers to planktivore/invertivore and Inv/Pisc refers to invertivore/piscivore. Legend applies to all panels.

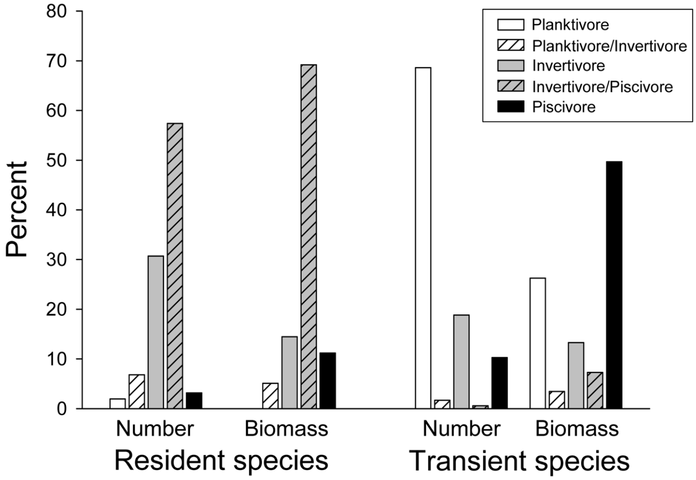

Figure 6. Percent contribution of different trophic groups in number and biomass to resident and transient (all non-resident taxa) fish communities associated with artificial reef study sites in the northeastern Gulf of Mexico.

Discussion

Perhaps the most striking result of the present study was the overwhelming dominance of reef fish communities by red snapper, which were nearly ubiquitous on study sites throughout the course of the sampling period and were even more dominant by biomass than by number. Red snapper density and biomass increased during the study, but both were high relative to other fishes throughout the study period. Despite this constancy with respect to red snapper's predominance, fish communities were temporally dynamic in species richness, trophic structure, overall fish density, and taxa-specific biomass of fishery species. Furthermore, the total number of species observed at reef sites during our study was greater than diversity observed in previous studies at artificial reefs of similar design and size both in the northern GOM (Strelcheck et al. 2005, Lingo and Szedlemayer 2006) and in other regions with comparable climate (Leitão et al. 2008).

Artificial reef sites were a little over 1 yr old when the present study began, thus were 4 yrs old at its conclusion. Previous research suggests that artificial reefs typically reach a mature, equilibrium community within 1–5 yrs (Bohnsack and Sutherland 1985). The development of complex fouling communities (e.g., macroalgae, bryozoans, sponges, and barnacles) as reef sites aged likely provided greater structural complexity and an increased forage base known to contribute to greater species diversity (Gratwicke and Speight 2005, Redman and Szedlmayer 2009). In a given year, species diversity was highest in summer, which coincided with an annual peak in the fouling community observed on reefs, as well as with the presence of tropical species not seen during other quarters.

Several factors can influence temporal changes in trophic structure and fish communities at artificial reefs beyond increased rugosity from fouling communities (Rooker et al. 1997). Among these are top-down predator control exerted by predators (Carr and Hixon 1995) and seasonal effects on hydrographic parameters or

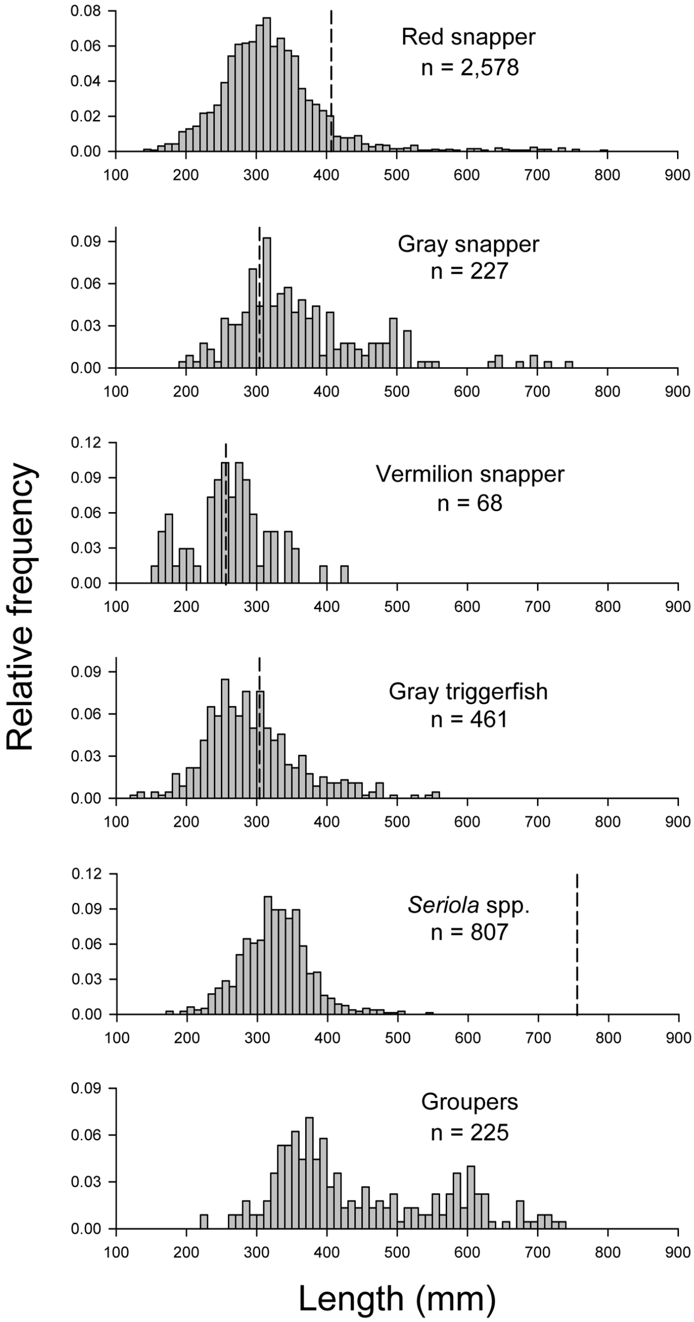

Figure 7. Length distributions of species for which significant fisheries exist observed at artificial reef sites in the northeastern Gulf of Mexico. Fork length is reported for gray triggerfish and *Seriola* spp. *Seriola* spp. includes greater amberjack (n = 661), almaco jack (n = 145), and lesser amberjack (n = 1). Groupers include scamp (n = 105), red grouper (n = 89), gag (n = 27), and snowy grouper (n = 4). Dashed vertical lines indicate minimum size limits in recreational fisheries for red snapper (406 mm TL), gray snapper (305 mm TL), vermilion snapper (254 TL), gray triggerfish (305 mm FL), and greater amberjack (762 mm FL)

recruitment (Bohnsack et al. 1994). Resident piscivores are known to affect the densities and size structure of fishes found at artificial reefs (Carr and Hixon 1995, Beets 1997, Hixon and Carr 1997). Though transient piscivores, such as greater amberjack, gradually replaced groupers as the predominant piscivores at study reefs, the decline of resident piscivores may have strongly influenced the changes in trophic structure of fishes present. Trophic assemblages, though dominated by invertivore/piscivores, such as red snapper, became more diverse over time with increased densities and biomass of lower trophic level fishes. Transient planktivores such as scads and sardines are known to be prey items for piscivores such as gag (Lindberg et al. 2006), and the proliferation of these taxa drove the increases in planktivore and fish density across time. While their presence is often infrequent, aggregations of transient planktivores can have a profound influence on fish communities at artificial reefs (Bohnsack et al. 1994). Furthermore, small invertivores, such as tomtate and red porgy, invertivore/planktivores, such as vermilion snapper and blue runner, and various small cryptic and juvenile fishes became more abundant and were observed more frequently after the decrease in resident piscivores. Success of lower trophic fishes, especially cryptic species, may be attributed to increased foraging opportunity and shelter afforded by reef attached organisms, but the results of the present study also indicate that these trophic groups may have been inhibited by high densities of resident piscivores earlier in the study.

Seasonal shifts in prey availability and processes of recruitment influenced temporal patterns in fish assemblages at study sites, as well as contributed to differences in trophic structure between resident and transient assemblages. The most consistently abundant fishes (red snapper and gray triggerfish) have diets that consist of either reef-attached organisms or benthic invertebrates and fishes associated with surrounding mud/sand substrates (Vose and Nelson 1994, Wells et al. 2008). Despite increasing in abundance, red snapper densities showed no distinguishable intra-annual seasonal patterns, which was consistent with other studies from the north-central GOM (Wells and Cowan 2007, Redman and Szedlmayer 2009). Species that exhibited variability in intra-annual and site-specific abundance were often dependent on pelagic prey, thus more subject to hydrographic processes. High variability in observed densities of planktivores among individual reef sites in our study may be attributed to local fluxes in plankton abundance. Zooplankton distributions and abundance are known to vary both across multiple time scales and vertically within a single diel period (Le Borgne et al. 2010, Heidelberg et al. 2010). Furthermore, large schools of transient planktivores, such as mackerel scad, round sardinella, and blue runner, may have also attracted transient piscivores, such as greater amberjack, all of which were observed in greater abundance in the latter part of the study. Intra-annual differences in amberjack abundance were likely due to recruitment pulses of sub-adult amberjack, which are known to transition from pelagic to demersal habitats (e.g., outcroppings and reefs) in the first year of life (Wells and Rooker 2004). Increased species richness, as well as variation in fish assemblages, are often attributed to an annual influx of juvenile recruits in the summer months (Rooker et al. 1997, Lingo and Szedlmayer 2006). Most individuals observed at reef sites in this study were sub-adults and adults; however, newly-settled and older age-0 fishes were encountered more frequently starting in the summer of 2006 and likely contributed to seasonal differences in fish community structure.

The most extreme taxa-specific shift that occurred during the study was the order of magnitude decline in grouper (gag, red grouper, and scamp) abundance during year one. It is possible that the passing of Hurricane Ivan through the study area in September 2004 redistributed groupers from offshore shelf-edge or other habitats to study reefs prior to the beginning of video sampling. Hurricanes have been shown previously to affect reef fish distributions (Turpin and Bortone 2002, Patterson et al. 2001), and increased grouper densities were observed on artificial reefs off South Carolina following Hurricane Hugo (Bell and Hall 1994). Similar to the present study, Bell and Hall (1994) also reported a subsequent steady decline in grouper densities as fishes either were removed by fishing pressure or they simply dispersed in the months following Hugo. Outside of potential storm effects, recent stock assessments indicated that gag and red grouper numbers experienced precipitous declines regionally from 2005 to 2006, which also may explain declines observed at study reefs. However, decreases in gag and red grouper spawning stock biomass estimates in the eastern GOM were attributed largely to a significant red tide event along the west Florida shelf that occurred hundreds of km to the southeast of reef sites examined in this study (SEDAR 2009a,b).

Effects of Reef Design.—Direct quantitative tests of factors, such as reef vertical relief, volume, hole size, and surface area, that possibly drove differences in fish communities among reef types, were not possible due to uncontrolled differences in reef design and dimensions. However, observed differences in fish communities among reefs are consistent with what would be predicted based on results of previous studies in which reef dimension and complexity were controlled (Hixon and Beets 1989, Beets and Hixon 1994, Lindberg et al. 2006). For example, A-type reefs in the present study were open structures with relatively high relief and few prefabricated hiding places. Although all reef designs supported high densities of invertivore/piscivores (primarily red snapper), trophic structure at A-type reefs was typified by high but variable densities of planktivores. Increased vertical relief at artificial reefs has been hypothesized to facilitate higher zooplankton concentrations (Rilov and Benyahu 2002, Arena et al. 2007), suggesting that planktivore abundance may be linked to higher vertical relief at A-type reefs vs the other two designs. Several species that feed high in the water column and are at least partially planktivorous, such as scad, round sardinella, blue runner, and vermilion snapper, were all observed at highest densities at A-type reefs. Alternatively, relatively lower densities of resident piscivores, such as groupers, at A-type reefs also may have contributed to the high mean abundance of some planktivores.

Ambush predators, such as groupers, typically prefer reefs that afford greater cover (Hixon and Beets 1989, Lindberg et al. 2006), which was lacking at A-type modules. This idea is reinforced by fish communities observed at two C-type reefs (C7 and C9) that were mostly buried and/or damaged following Hurricane Rita in September 2005, thus leaving little surface area for fouling growth and a lack of cover for larger fishes. Thereafter, those two sites had consistently higher densities of transient planktivores, small reef residents, and juvenile fishes, and an absence of groupers or other large piscivores, relative to other C-type reefs.

Greater surface area at B-type reefs promoted growth of barnacles and other sessile reef-attached invertebrates, adding more structural complexity and rugosity to the habitat, which resulted in greater reef fish diversity than the other two reef types. Previous studies have also shown that complex three dimensional habitat can promote species richness (Rooker et al. 1997, Lingo and Szedlmayer 2006, Redman and Szedlmayer 2009). Increased invertivore biomass at B-type reefs was mostly attributed to elevated gray triggerfish abundance, a species which has been shown to feed disproportionately on barnacles and encrusting organisms at artificial reef sites (Vose and Nelson 1994). Greater structural complexity afforded by fouling communities likely also benefitted gray snapper, a species commonly associated with coral reefs and found at higher densities at B-type reefs (Burton 2001). While the increased surface area appeared to encourage settlement of sessile organisms, including algae, herbivores were practically non-existent at study sites, a finding consistent with the artificial reef literature (Bohnsack et al. 1994, Thanner et al. 2006). Lastly, reef spacing was an uncontrolled issue with paired B-type modules, and our conservative estimates of fish density and biomass due to this factor may have down-weighted some of the distinctiveness of fish communities at this reef type.

C-type modules had well-defined holes, a hollow central cavity, and a higher surface area to volume ratio to promote fouling communities. These characteristics perhaps offered greater habitat complexity and shelter for resident piscivores (Hixon and Beets 1989, Beets and Hixon 1994, Lingo and Szedlmayer 2006). As many as six gag were observed on multiple occasions in the central cavity of one C-type module, a phenomenon not observed at other reef types, despite their larger volumes compared to C-type modules. Lindberg et al. (2006) also frequently observed multiple gag retreating and hiding inside the central internal cavities of artificial reef modules in the northeastern GOM, and they reported that high gag density actually had a negative, density-dependent effect on growth. Lastly, condition of C-type reefs was more variable than other reef types which likely contributed to disparity in fish communities within reefs of this design. Reef fish communities at sites partially buried after Hurricane Rita more closely resembled those previously described at shell rubble habitats and low vertical relief structure in the northern GOM (Wells and Cowan 2007, Wells et al. 2009).

Size-Structure of Fishery Species.—The size structure of fishery species has great relevance for inferring the ecological function of artificial reefs, as well as determining the efficacy of unreported reefs to serve as no-harvest refugia or as potential sources (vs sinks) of recruits to other habitats (Bohnsack and Sutherland 1985, Bohnsack et al. 1994, Crowder et al. 2000). Species that display high site fidelity would be more likely to display enhanced production from artificial reef creation than species that do not, especially if not reporting reef coordinates successfully precludes fishing at created reefs (Bohnsack 1989, Willis and Millar 2005). Therefore, species that display high site fidelity would be expected to have broad size distributions representative of several age classes present on reefs. In fact, species such as gray triggerfish, vermilion snapper, and gray snapper that are known to display high site fidelity to reefs (Burton et al. 2001, Ingram and Patterson 2001, Allman 2007) also were characterized by having wide size distributions in the present study. Moreover, relatively high percentages of individuals of these species exceeded the legal size limit in the recreational fishery, the predominant fishing sector targeting reef fishes in the study area. Therefore, it appears gray triggerfish, vermilion snapper, and gray snapper experienced minimal if any fishing mortality at unreported study reefs, which is corroborated by the fact that no evidence of fishing was observed at study reefs (e.g., no hooks or line observed fouling reefs, and no vessels observed at study sites during sampling trips).

Fishes known to display temporary residency or low annual site fidelity, such as amberjack (Ingram and Patterson 2001), groupers (Lindberg et al. 2006), and red snapper (Patterson and Cowan 2003), were characterized by truncated size distributions consisting of mostly small, young fishes. While it is not known why individuals of these species often disappeared from study sites before reaching large sizes, we suggest three possible scenarios. First, the lack of larger, older fishes simply may have reflected ontogenetic movement away from study reefs. If fishing occurred at study sites, then direct removal of larger fishes could have occurred. Lastly, if fishes moved among habitats, then their size distributions may have reflected regional size structure affected by fishing pressure away from study reefs.

Ontogenetic shifts in habitat utilization are well documented for many reef fish taxa (Koenig et al. 2000, Wells and Rooker 2004), and shifts in the size distributions of certain species observed during this study clearly could be attributed to ontogeny. Greater amberjack size distribution was the most limited of all fishery species (mode 250–350 mm FL), with fish sizes indicating virtually all observed individuals were age-1 or -2 (Thompson et al. 1999), and none approached the recreational size limit of 762 mm FL. The observation that study sites were occupied only by sub-adult amberjack not yet recruited to the fishery (Ingram and Patterson 2001, Wells and Rooker 2004) indicates that amberjack may utilize reefs as transitional habitat before moving to larger offshore structures. Species such as snowy grouper, speckled hind, and warsaw grouper were only observed at study sites as small juveniles; therefore, they also likely used study sites as transitional habitat, a trend previously documented in deepwater groupers (Arena et al. 2007). Groupers such as gag, scamp, and red grouper are protogynous hermaphrodites known to utilize mid-shelf artificial reefs as pre-reproductive females transitioning across the shelf as they mature (Koenig et al. 2000, Lindberg et al. 2006). Pre-reproductive females can vary in size considerably and may attain large sizes at mid-shelf reefs (Koenig et al. 2000), and many groupers were larger than legal sizes for retention. However, it is still most likely that groupers utilized study reefs only as transitional habitat prior to moving farther offshore.

There is evidence that red snapper also undergo ontogenetic shifts in habitat utilization towards deeper shelf-edge reefs or other habitats as they age (Mitchell et al. 2004, Gallaway et al. 2009). Larger, older red snapper were conspicuously absent from reefs examined in the present study, which may indicate that fish moved to other habitats as they aged. However, there was no trend in red snapper size with depth among study reefs that ranged in depth from 27 to 41 m. Moreover, red snapper size distribution dropped markedly right at the legal size limit for the recreational fishery, thus implicating a fishery effect rather than ontogenetic movement. This inference is further supported by results of fishery-independent sampling that indicate older (> 10 yrs) red snapper are an order of magnitude less abundant in the north central GOM vs the stock's center of abundance off southwestern Louisiana (Gledhill 2001, Mitchell et al. 2004), a trend that has been attributed to exceedingly high apical fishing mortality rates (0.7–0.9 yr^{-1}) in the recreational fishery in the north central GOM (Porch 2007, SEDAR 2009c).

The question remains whether fish were targeted at study reefs vs elsewhere if the red snapper size distribution observed at study reefs was due to fishing mortality. As stated above, we have no direct evidence of fishing at study sites. Furthermore, other species that are targeted by the recreational fishery with the same gear as red snapper did not display size distributions truncated at fishery size limits. A key difference is that these other species, such as gray triggerfish, vermilion snapper, and gray snapper, are known to display high site fidelity to reefs while red snapper site fidelity has been estimated as only 25%–50% yr^{-1} to artificial reefs in the northern GOM (Patterson and Cowan 2003, Schroepfer and Szedlmayer 2006, Strelcheck et al. 2007). Intense fishing pressure near marine reserves has been shown to negatively impact the size structure (i.e., a greater proportion of sub-legal fish) and abundance of exploited species that move between protected and unprotected areas, thus reducing the effectiveness of reserves (Larsen 2005, Willis and Millar 2005). Mean distances moved by red snapper tagged at artificial reefs in the northern GOM range from 10–25 km yr^{-1} (Patterson et al. 2001, Strelcheck et al. 2007, Addis et al. 2008), and even small scale movements (< 5 km) of red snapper among artificial reefs within the EE-LAARS could have exposed fish to high regional fishing mortality. Therefore, it appears unlikely that red snapper benefitted as much as other species from a lack of fishing pressure at study reefs given the likelihood that they were moving among fished and unfished reefs.

Overall, results from the present study suggest that unreported artificial reef sites can support diverse fish communities in the northern GOM. Fish assemblages, species diversity, and trophic structure at study sites were dynamic across time and among reef designs, despite the predominance of age-2 to age-3 red snapper at all sites. Truncated size distributions of many fishery species, such as red snapper, greater amberjack, and several groupers, that indicate individuals disappeared from study sites with size or age, is worrisome considering that study reefs were deployed to serve as no-harvest refugia, thus as sources vs sinks for these species. To properly site and utilize artificial reefs as mitigating tools within protected areas (Wilson et al. 2002), managers need to consider patterns of movement and habitat use at multiple spatial scales for fishery species as success of any marine reserve depends on the geographic extent needed to encompass the range of habitats utilized by exploited species (Crowder et al. 2000, Willis and Millar 2005). Results from our study suggest that artificial reefs should not be viewed as isolated habitats, but as part of a larger regional network of habitats (Grossman et al. 1997). Given the prevalence of artificial reef deployment in the northern GOM, there is a growing need for comprehensive experimental research and long-term monitoring to better understand how these habitats function ecologically and as fishery tools. The present study provides an important baseline for future research in the EE-LAARS aimed at this question, and also may prove to be useful for examining the impact of the Deepwater Horizon oil spill on reef fishes in this region of the GOM.

Acknowledgments

This research was funded by Florida Fish and Wildlife Conservation Commission (Grants FWCC-04032, -05027, and -06120 to WFP) with special thanks to K Mille and J Dodrill. Research was conducted aboard the F/V Dorado, and we thank Captain J Theirry for his contribution to this study. W Lindberg and P Darby provided valuable suggestions and advice which improved the quality of this study and manuscript. We also thank N Morris, K Shepard, and C Lounder for field assistance.

Literature Cited

Addis DT, Patterson WF III, Dance MA. 2008. Site fidelity and movement of reef fishes tagged at unreported artificial reef sites off northwest Florida. Proc Gulf Caribb Fish Inst. 60:297–304.

Allman RJ. 2007. Small-scale spatial variation in the population structure of vermilion snapper (*Rhomboplites aurorubens*) from the northeast Gulf of Mexico. Fish Res. 88:88–99. http://dx.doi.org/10.1016/j.fishres.2007.07.017

Arena PT, Jordan LKB, Spieler RE. 2007. Fish assemblages at sunken vessels and natural reefs in southeast Florida, USA. Hydrobiologia. 580:157–171. http://dx.doi.org/10.1007/s10750-006-0456-x

Baine M. 2001. Artificial reefs: a review of their design, application, management, and performance. Ocean Coast Manage. 44:241–259. http://dx.doi.org/10.1016/S0964-5691(01)00048-5

Beets JP. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar Ecol Prog Ser. 148:11–21. http://dx.doi.org/10.3354/meps148011

Beets JP, Hixon MA. 1994. Distribution, persistence, and growth of groupers (Pisces, Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bull Mar Sci. 55:470–483.

Bell M, Hall JW. 1994. Effects of Hurricane Hugo on South Carolina's marine artificial reefs. Bull Mar Sci. 55:836–847.

Bohnsack JA. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation of behavioral preference? Bull Mar Sci. 44:631–644.

Bohnsack JA, Sutherland DL. 1985. Artificial reef research: a review with recommendations for future priorities. Bull Mar Sci. 37:11–39.

Bohnsack JA, Harper DE. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. NOAA Technical Memoir NMFS-SEFC-215. 31 p.

Bohnsack JA, Harper DE, McClellan DB, Hulsbeck M. 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. Bull Mar Sci. 55:796–823.

Burton ML. 2001. Age, growth, and mortality of gray snapper, *Lutjanus griseus,* from the east coast of Florida. Fish Bull. 99:254-265.

Carr MH, Hixon MA. 1995. Predation effects on early postsettlement survivorship of coral reef fishes. Mar Ecol Prog Ser. 124:31–42. http://dx.doi.org/10.3354/meps124031

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Aust J Ecol. 18:117–143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Gorley RN. 2001. PRIMER v5: user manual/tutorial. PRIMER-E Ltd., Plymouth, United Kingdom.

Crowder LB, Lyman SJ, Figueira WF, Priddy J. 2000. Source sink population dynamics and the problem of siting marine reserves. Bull Mar Sci. 66:799–820.

Drass DM, Bootes KL, Lyczkowski-Schultz J, Comyns BH, Holt GJ, Riley CM, Phelps RP. 2000. Larval development of red snapper, *Lutjanus campechanus,* and comparisons with co-occurring snapper species. Fish Bull. 98:507–527.

Gallaway BJ, Szedlmayer ST, Gazey WJ. 2009. Snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Rev Fish Sci. 17:48–67. http://dx.doi.org/10.1080/10641260802160717

Gledhill CT. 2001. Reef fish assemblages on Gulf of Mexico shelf-edge banks. PhD dissertation. University of South Alabama. 193 p.

Gratwicke B, Speight MR. 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Mar Ecol Prog Ser. 292:301–310. http://dx.doi.org/10.3354/meps292301

Grossman GD, Jones GP, Seaman Jr WJ. 1997. Do artificial reefs increase regional fish production? A review of existing data. Fisheries. 22(4):17–23. http://dx.doi.org/10.1577/1548-8446(1997)022<0017:DARIRF>2.0.CO;2

Heidelberg KB, O'Neil KL, Bythell JC, Sebens KP. 2010. Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). J Plankton Res. 32:75–91. PMid:20046854. PMCid:2787388. http://dx.doi.org/10.1093/plankt/fbp101

Hixon MA, Beets JP. 1989. Shelter characteristics and Caribbean fish assemblages—experiments with artificial reefs. Bull Mar Sci. 44:666–680.

Hixon MA, Carr MH. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science. 277:946–949. http://dx.doi.org/10.1126/science.277.5328.946

Ingram GW, Patterson III WF. 2001. Movement patterns of red snapper (*Lutjanus campechanus*), greater amberjack (*Seriola dumerili*), and gray triggerfish (*Balistes capriscus*) in the Gulf of Mexico and the utility of marine reserves as management tools. Proc Gulf Caribb Fish Inst. 52:686–699.

Koenig CC, Coleman FC, Grimes CB, Fitzhugh GR, Scanlon KM, Gledhill CT, Grace M. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. Bull Mar Sci. 66:593–616.

Larsen SJ. 2005. Influence of high-resolution spatial information on resource exploitation: an example from angler impacts on artificial reefs. MS Thesis. University of Florida. 53 p.

Le Borgne R, Douillet P, Fichez R, Torreton J. 2010. Hydrography and plankton temporal variabilities at different time scales in the southwest lagoon of New Caledonia: a review. Mar Pollut Bull. 61:297–308. PMid:20638087. http://dx.doi.org/10.1016/j.marpolbul.2010.06.022

Leitão F, Santos MN, Erzini K, Monteiro CC. 2008. Fish assemblages and rapid colonization after enlargement of an artificial reef off the Algarve coast (southern Portugal). Mar Ecol. 29:435–448. http://dx.doi.org/10.1111/j.1439-0485.2008.00253.x

Lindberg WJ. 1997. Can science solve the attraction versus production debate? Fisheries. 22(4):10–13.

Lindberg WJ, Frazer TK, Portier KM, Vose F, Loftin J, Murie DJ, Mason DM, Nagy B, Hart MK. 2006. Density-dependent habitat selection and performance by a large mobile reef fish. Ecol Appl. 16:731–746. http://dx.doi.org/10.1890/1051-0761(2006)016[0731:DHSAPB]2.0.CO;2

Lingo ME, Szedlmayer ST. 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. Env Biol Fish. 76:71–80. http://dx.doi.org/10.1007/s10641-006-9009-4

Minton V, Heath SR. 1998. Alabama's artificial reef program: building oases in the desert. Gulf Mex Sci. 16:105–106.

Mitchell KM, Henwood T, Fitzhugh GR, Allman RJ. 2004. Distribution, abundance, and age structure of red snapper (*Lutjanus campechanus*) caught on research longlines in US Gulf of Mexico. Gulf Mex Sci. 22:164–172.

Nelson RS, Manooch CS. 1982. Growth and mortality of red snappers in the west-central Atlantic Ocean and northern Gulf of Mexico. Trans Am Fish Soc. 111:465–475. http://dx.doi.org/10.1577/1548-8659(1982)111<465:GAMORS>2.0.CO;2

Osenberg CW, St. Mary CM, Wilson JA, Lindberg WJ. 2002. A quantitative framework to evaluate the attraction-production controversy. ICES J Mar Sci. 59:214–221. http://dx.doi.org/10.1006/jmsc.2002.1222

Patterson III WF, Cowan Jr JH. 2003. Site fidelity and dispersion of red snapper associated with artificial reefs in the northern Gulf of Mexico. *In:* Stanley D, Scarborough-Bull A, editors. Fisheries, reefs, and offshore development. American Fisheries Society, Symposium 36. Bethesda, Maryland. p. 181–194.

Patterson III WF, Dance MA, Addis DT. 2009. Development of a remotely operated vehicle based methodology to estimate fish community structure at artificial reef sites in the northern Gulf of Mexico. Proc Gulf Caribb Fish Inst. 61:263–270.

Patterson III WF, Watterson JC, Shipp RL, Cowan Jr JH. 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Trans Am Fish Soc. 130:533–545. http://dx.doi.org/10.1577/1548-8659(2001)130<0533:MOTRSI>2.0.CO;2

Porch CE. 2007. An assessment of the red snapper fishery in the US Gulf of Mexico using a spatially-explicit age-structured model. *In:* Patterson III WF, Cowan Jr JH, Nieland DA, Fitzhugh GR, editors. Population ecology and fisheries of US Gulf of Mexico red snapper. American Fisheries Society. Bethesda, Maryland. p. 355–384.

Redman RA, Szedlmayer ST. 2009. The effects of epibenthic communities on reef fishes in the northern Gulf of Mexico. Fish Manage Ecol. 16:360–367. http://dx.doi.org/10.1111/j.1365-2400.2009.00684.x

Rilov G, Benayahu Y. 2002. Rehabilitation of coral reef-fish communities: the importance of artificial-reef relief to recruitment rates. Bull Mar Sci. 70:185–197.

Rooker JR, Dokken QR, Pattengill CV, Holt GJ. 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. Coral Reefs. 16:83–92. http://dx.doi.org/10.1007/s003380050062

SAS (SAS Institute, Inc.). 2004. Statistics Version 9.1. SAS Institute Inc., Cary, North Carolina.

Schroepfer RL, Szedlmayer ST. 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico. Bull Mar Sci. 78:93–101.

SEDAR (Southeast Data Assessment and Review). 2009a. Report of Assessment Workshop, Stock Assessment of Gag in the Gulf of Mexico: SEDAR Update Assessment. Available from: SEDAR http://www.sefsc.noaa.gov/sedar/. Charleston, South Carolina. 171 p.

SEDAR (Southeast Data Assessment and Review). 2009b. Report of Assessment Workshop, Stock Assessment of Red Grouper in the Gulf of Mexico: SEDAR update assessment. Available from: SEDAR http://www.sefsc.noaa.gov/sedar/. Charleston, South Carolina. 143 p.

SEDAR (Southeast Data Assessment and Review). 2009c. Report of Assessment Workshop, Stock Assessment of Red Snapper in the Gulf of Mexico: SEDAR Update Assessment. Available from: SEDAR http://www.sefsc.noaa.gov/sedar/. Miami, Florida. 224 p.

Shipp RL, Bortone SA. 2009. A prospective of the importance of artificial habitat on the management of red snapper in the Gulf of Mexico. Rev Fish Sci. 17:41–47. http://dx.doi.org/10.1080/10641260802104244

Spanier E, Barshaw D. 1994. Artificial habitats function as protection against a natural predator for commercial species. Bull Mar Sci. 55:2–3.

Stone RB, Sprague LM, McGurrin JM, Seaman Jr W. 1991. Artificial habitats of the world: synopsis and major trends. *In:* Seaman W, Sprague L, editors. Artificial habitats for marine and freshwater fisheries. Academic Press, San Diego. p. 31–57.

Strelcheck AJ, Cowan Jr JH, Patterson III WF. 2007 Site fidelity, movement, and growth of red snapper: implications for artificial reef management. *In:* Patterson III WF, Cowan Jr JH, Nieland DA, Fitzhugh GR, editors. Population ecology and fisheries of US Gulf of Mexico red snapper. American Fisheries Society. Bethesda, Maryland. p. 135–148.

Strelcheck AJ, Cowan Jr JH, Shah A. 2005. Influence of reef location on artificial-reef fish assemblages in the northcentral Gulf of Mexico. Bull Mar Sci. 77:425–440.

Thanner S, McIntosh T, Blair S. 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. Bull Mar Sci. 78:57–70.

Thompson BA. 1999. Age distribution and growth of greater amberjack, *Seriola dumerili,* from the north-central Gulf of Mexico. Fish Bull. 97:362–371.

Turpin RK, Bortone SA. 2002. Pre- and post-hurricane assessment of artificial reefs: evidence for potential use as refugia in a fishery management strategy. ICES J Mar Sci. 59:74–82. http://dx.doi.org/10.1006/jmsc.2002.1191

Vose FE, Nelson WG. 1994. Gray triggerfish (*Balistes capriscus* Gmelin, 1789) feeding from artificial and natural substrate in shallow Atlantic waters of Florida. Bull Mar Sci. 55:796–823.

Wells RJD, Rooker JR. 2004. Spatial and temporal patterns of habitat use by fishes associated with Sargassum mats in the northwestern Gulf of Mexico. Bull Mar Sci. 74:81–99.

Wells RJD, Cowan Jr JH. 2007. Video estimates of red snapper and associated fish assemblages on sand, shell, and natural reef habitats in the north-central Gulf of Mexico. *In:* Patterson

III WF, Cowan Jr JH, Nieland DA, Fitzhugh GR, editors. Population ecology and fisheries of US Gulf of Mexico red snapper. American Fisheries Society. Bethesda, Maryland. p. 39–58.

Wells RJD, Cowan Jr JH, Fry B. 2008. Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Mar Ecol Prog Ser. 361:213–225. http://dx.doi.org/10.3354/meps07425

Wells RJD, Harper JO, Rooker JR, Landry Jr AM, Dellapenna TM. 2009. Fish assemblage structure on a drowned barrier island in the northwestern Gulf of Mexico. Hydrobiologia. 625:207–221. http://dx.doi.org/10.1007/s10750-009-9709-9

Willis TJ, Millar RB. 2005. Using marine reserves to estimate fishing mortality. Ecol Lett. 8:47–52. http://dx.doi.org/10.1111/j.1461-0248.2004.00692.x

Wilson KDP, Leung AWY, Kennish R. 2002. Restoration of Hong Kong fisheries through deployment of artificial reefs in marine protected areas. ICES J Mar Sci. 59:157–163. http://dx.doi.org/10.1006/jmsc.2002.1186

Zhao B, McGovern JC, Harris PJ. 1997. Age, growth, and temporal change in size at age of the vermilion snapper from the South Atlantic Bight. Tran Am Fish Soc. 126:181–193. http://dx.doi.org/10.1577/1548-8659(1997)126<0181:AGATCI>2.3.CO;2

Date Submitted: 10 May, 2010.
Date Accepted: 17 February, 2011.
Available Online: 18 March, 2011.

Addresses: (MAD, WFP, DTA) *University of West Florida, Biology Department, Bldg. 58, 11000 University Parkway, Pensacola, Florida 32514.* Present Addresses: (MAD) *Department of Marine Biology, Texas A&M University at Galveston, 200 Seawolf Pkwy OCSB Bldg 3029, Galveston, Texas 77553.* (DTA) *Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Ave. S.E., St. Petersburg, Florida 33701.* Corresponding Author: (MAD) *E-mail*: *<dancema@tamu.edu>.*