A Comparison of Fish Assemblages According to Artificial Reef Attributes and Seasons in the Northern Gulf of Mexico

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SEDAR74-RD09

November 2020

American Fisheries Society Symposium 86:23–45, 2018

A Comparison of Fish Assemblages According to Artificial Reef Attributes and Seasons in the Northern Gulf of Mexico

Jessica Jaxion-Harm, Stephen T. Szedlmayer*, and Peter A. Mudrak
School of Fisheries, Aquaculture and Aquatic Sciences, Auburn University
8300 State Highway 104, Fairhope, Alabama 36532, USA

Abstract.—Visual census scuba surveys (n = 87) were used to compare fish assemblages among three artificial reef types: big reefs (e.g., ships), tank reefs (i.e., U.S. Army tanks) and small reefs (e.g., metal cages and concrete pyramids), over three locations on the continental shelf (inner shelf, 18–26-m depths; mid-shelf, 26–34-m depths; outer shelf, 34–41-m depths) from April 20, 2012 to November 30, 2015 in the northeast Gulf of Mexico. These surveys identified 66 fish taxa (lowest taxon: 58 species, five genera, three families), and 65 taxa were used in community comparisons. Artificial reefs were dominated by Red Snapper *Lutjanus campechanus* (35.3% of total fish observed), Tomtate *Haemulon aurolineatum* (22.4%), Vermilion Snapper *Rhomboplites aurorubens* (19.5%), Atlantic Spadefish *Chaetodipterus faber* (7.0%), Greater Amberjack *Seriola dumerili* (3.0%), and Gray Triggerfish *Balistes capriscus* (1.8%). These six most abundant species comprised 89% of the total number of individuals observed. Red Snapper and Greater Amberjack mean sizes (total length mm) were larger at big reefs, Vermilion Snapper and Atlantic Spadefish were larger at tank reefs, and Tomtates were larger at small reefs. Red Snapper, Atlantic Spadefish, and Greater Amberjacks were larger at reefs on the outer shelf, and Red Snapper, Tomtates, Vermilion Snapper, Atlantic Spadefish and Greater Amberjacks were larger in the spring. Richness and Shannon–Wiener diversity indices were higher on big reefs and tank reefs compared to small reefs. Evenness, richness, and Shannon–Wiener diversity were lower in winter compared to other seasons. Fish assemblages, based on Bray–Curtis similarities, were different among reef type, location, and season, but no interactions effects were identified. In the present study, fish assemblages on big reefs were more similar to assemblages on tank reefs in comparison to small reefs. The larger size, longer life span, and relative stability of the big reefs and tank reefs were the reef attributes most likely responsible for these assemblage associations. Similarly, more stable conditions at deeper depths (less affected by tropical storms) and proximity to deepwater reef fish communities (e.g., pinnacle reefs) most likely influenced

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* Corresponding author: szedlst@auburn.edu

the increased assemblage diversity on the artificial reefs at outer-shelf locations. Diversities and densities were highest during the fall. This was most likely due to increased recruitment of tropical species and new age-0 recruits that were spawned during the same year. The attributes of all artificial reefs are not identical; consequently, it is important for managers to consider how reef type, shelf location, and season affect each species' affinity and association with artificial reefs.

Introduction

Artificial reefs are deployed to achieve various objectives (e.g., facilitate habitat mitigation, prevent trawling, and enhance fisheries), but ultimately, they provide hard substrate that can potentially increase the stock size of fish species (Baine 2001; Gallaway et al. 2009; Shipp and Bortone 2009; Smith et al. 2015). Hard-structure habitats can provide protection from predators and increase food resources from the growth of epibenthic communities (Hixon and Beets 1993; Redman and Szedlmayer 2009). Historically, deploying artificial reefs for enhancing fish production has focused on individual fish species (Lindberg et al. 2006; Shipp and Bortone 2009), but deploying artificial reefs to achieve the objectives of ecosystem-based management has recently become more prevalent (Crowder et al. 2008; deReynier et al. 2010). For example, the loss of biodiversity in marine systems has negatively affected ecosystem stability and production (Worm et al. 2006). Additionally, Pickering et al. (1998) suggested that one potential approach to help increase biodiversity is to deploy artificial reefs.

In the northeast Gulf of Mexico, there are few natural reefs (Dufrene 2005; Jenkins et al. 2008; Williams et al. 2012). Thus, the deployment of artificial reefs can increase available reef-like habitat and possibly increase faunal diversity of species that are reef-associated (Lingo and Szedlmayer 2006; Gallaway et al. 2009). Historical evidence suggests that reef species such as Red Snapper *Lutjanus campechanus* have become more abundant subsequent to artificial reef deployments on the sand-mud substrate of the continental shelf in the northern Gulf of Mexico (Gallaway et al. 2009; Shipp and Bortone 2009). There has been extensive research depicting artificial reefs as fish attractors and potential producers (Bohnsack and Sutherland 1985; Pickering and Whitmarsh 1997; Bortone et al. 2011), yet few studies have examined fish assemblages on substantially different types of artificial reefs in the northern Gulf of Mexico (Stanley and Wilson 1997; Lingo and Szedlmayer 2006; Dupont 2008; Dance et al. 2011; Ajemian et al. 2015). For example, studies have examined concrete pyramids and reef balls (Dance et al. 2011), small 1-m^3 concrete blocks (Lingo and Szedlmayer 2006), and oil platforms (Stanley and Wilson 1997; Ajemian et al. 2015). Yet, a variety of artificial reefs have been deployed in the northeast Gulf of Mexico that differ in size and complexity, from small concrete pyramids and metal cages to large ships and oil-gas platforms.

As the deployment of reefs increases (McGurrin et al. 1989; Bohnsack et al. 1994), it is necessary to consider both reef type and location in relation to fish assemblages that recruit to these artificial structures. Thus, an important new aspect of the present study was the examination of fish assemblages over diverse artificial reef types. In addition, the present study examined artificial reefs over much of the continental shelf as distributions of many fish species are depth-related (Gul et al. 2011; Sherman et al. 1999). Specifically, the present study examined different artificial reef types over three shelf areas: inner shelf (18–26-m depths), mid-shelf (26–34-m depths), and outer-shelf (34–41-m depths), to provide a better understanding of fish assemblages and densities of juvenile and adult fishes that associate with these artificial reef habitats. Such information will help managers with the difficult decisions to employ artificial reefs in fishery resource management and give direction to future reef research efforts.

Methods

Study Area

The study area was located 16–64 km south of Mobile Bay, Alabama (USA), in the northern Gulf of Mexico. All reefs were from three locations on the continental shelf over three depth zones (inner shelf, 18–26 m; mid-shelf, 26–34 m; and outer shelf, 34–41 m). Artificial reef types that were surveyed included concrete pyramids, army tanks, concrete rubble, metal cages, barges, gas platforms, ships, and several other miscellaneous structures. All reefs were separated into three categories: big reefs (2,500–3,800 m^3; e.g., ships, gas platforms), mid-size tank reefs (volume = 51 m^3; i.e., U.S. Army tanks), and small reefs (volume = 4–15 m^3; e.g., pyramids). Both public reefs (i.e., reefs with published locations made available to fishers by the Alabama Department of Conservation and Natural Resources) and private reefs (locations usually known only to the builder) were investigated in the present study. Unpublished or private reefs were located with side-scan sonar surveys (Edgetech 4125-Dual 400/900 Hz). Private reefs consisted of a wide variety of structures, from metal cages to concrete rubble. Stratified random sampling was used to select reefs among the three shelf locations and three artificial reef types (big reefs, tank reefs, and small reefs). Sample sites were selected using a random numbers table from a total of 835 identified reef structures (268 private reefs located with the side-scan surveys and 567 public reef sites). A total of 87 artificial reef sites were surveyed from 16 to 64 km offshore of coastal Alabama (Figure 1). These included 23 big reefs (8 inner shelf, 8 mid-shelf, and 7 outer shelf), 24 tank reefs (5 inner shelf, 11 mid-shelf, and 8 outer shelf), and 40 small reefs (14 inner shelf, 11 mid-shelf, and 15 outer shelf). To evaluate seasonal differences in the reef-associated fish assemblages, surveys were conducted during the spring (22 surveys), winter (10), summer (26), and fall (29), pooled over reef types and locations from April 20, 2012 to November 30, 2015 (Figure 2).

Fish Surveys

Divers (using scuba) estimated fish length to the nearest 25 mm total length (TL) using a stationary point-count method during the day (from 2 h before to 4 h after 1200 hours) to calculate fish densities (Greene and Alevizon 1989). Water clarity was determined using horizontal measures of a Secchi disk during each survey. The composition material and size of each reef were also recorded at each site. A YSI 6920 environmental meter was used to measure temperature (°C), salinity (‰), and dissolved oxygen (mg/L) within 2 m of the bottom and less than 20 m of each reef site.

The area surveyed was calculated by using a maximum radius of 6 m for density estimations when horizontal water clarity exceeded 6 m from the Secchi disk measure-

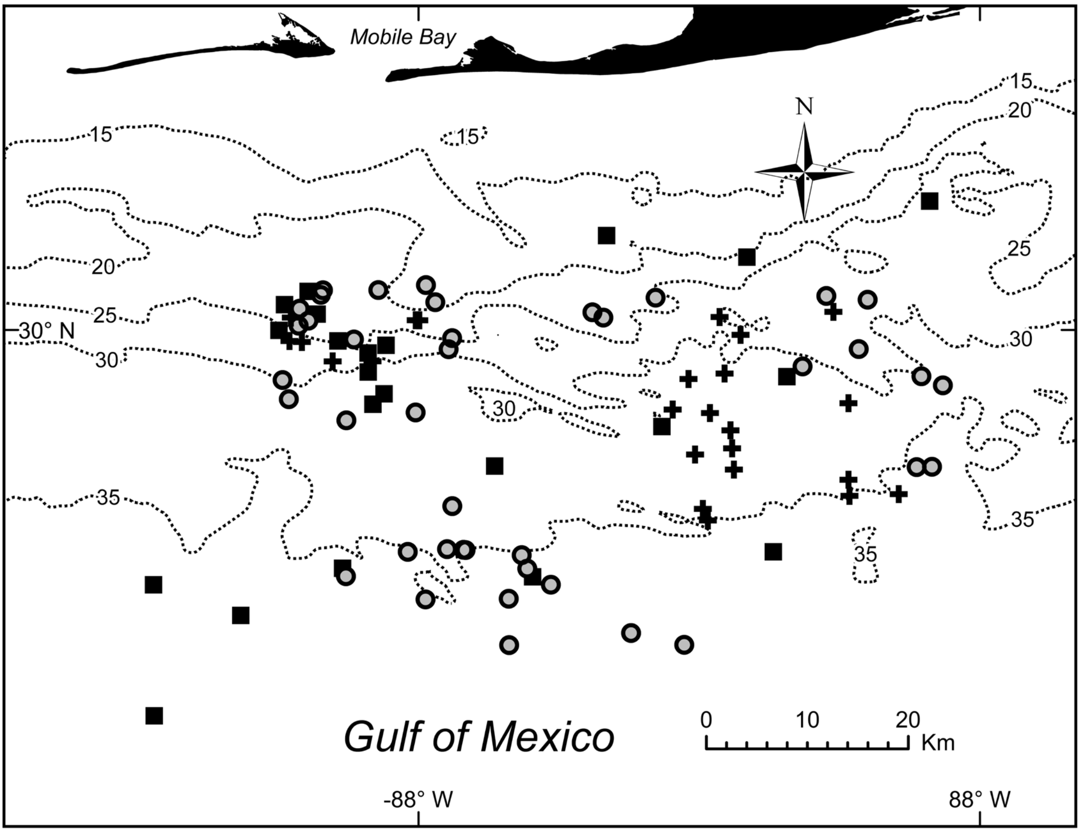

Figure 1. Artificial reef study sites in the northern Gulf of Mexico. Big reefs = squares, tank reefs = crosses, and small reefs = gray dots. Dotted lines represent depth contours at 5-m intervals.

ment. The maximum 6-m radius was selected as the distance that divers could accurately identify fish species and estimate fish lengths. When visibility was between 3 and 6 m, the Secchi disk visibility distance was used as the radius for area-surveyed calculations. If visibility was less than 3 m, the survey data were not included in the analyses (10 sites were removed out of 97 sites = 87 survey sites). Fish density (number of fish/100 m^2) was calculated for each site surveyed.

Statistical Analyses

Diversity indices were compared relative to the independent variables: reef type, shelf location, and season (winter = December–February, spring = March–May, summer = June–August, and fall = September–November) using analyses of variance (ANOVAs; SAS version 9.4; Zar 2010). Densities of fish were square-root-transformed prior to calculations of diversity measures (Field et al. 1982). Fish communities were compared using the Shannon–Wiener diversity index (H'), richness (S), and evenness ($J = H'/H'\text{max}$; Magurran 1988).

Fish densities (number of fish/100 m^2) were compared using generalized linear models (PROC GENMOD, SAS version 9.4) with negative binomial distributions and log link functions (Huelsenbeck and Crandall 1997; Seavy et al. 2005; Bolker et al. 2009). The statistical model examined all main effects and interactions, but after analyses,

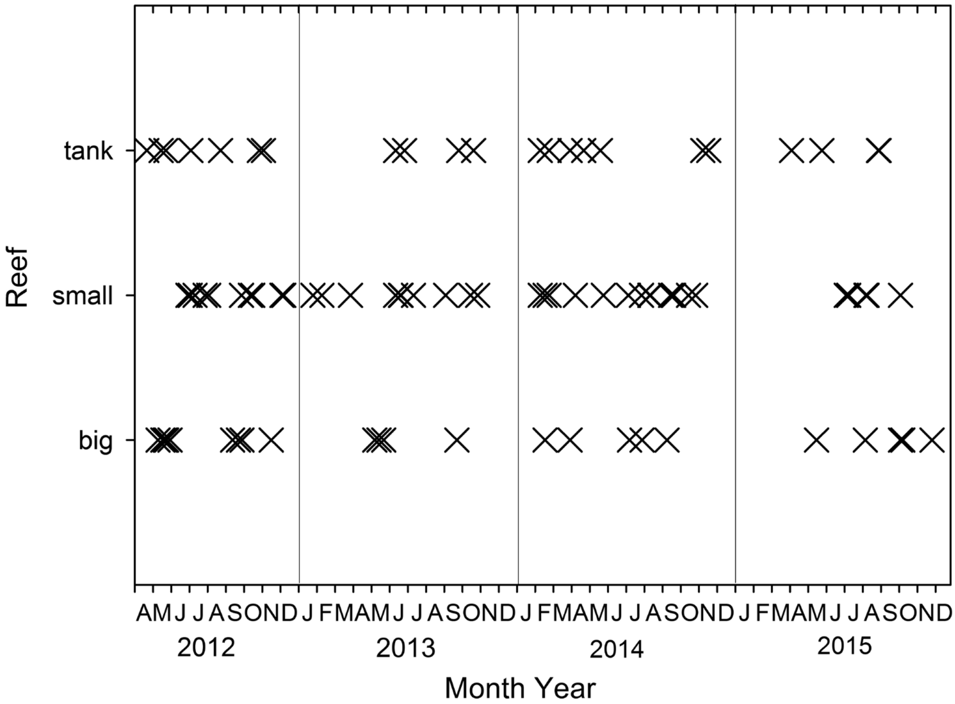

Figure 2. Sampling frequency by month and year for fish assemblage surveys on artificial reefs in the northern Gulf of Mexico.

most three-way interactions were excluded because of the small sample sizes in three factor cells.

Densities of fish species were square-root-transformed prior to calculations of Bray–Curtis similarities (Field et al. 1982). These similarity indices were compared among all surveys and visually examined with nonmetric multidimensional scaling (MDS) ordination plots (Bray and Curtis 1957; Clarke and Green 1988; Szedlmayer and Able 1996; Lingo and Szedlmayer 2006). The MDS plots spatially indicates the relative similarity (or dissimilarity) of reef fish assemblages. The fish assemblage similarities among all individual reef surveys were examined statistically among reef types, shelf locations, and seasons with three-way permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson et al. 2008).

Environmental variables (temperature, salinity, dissolved oxygen, and depth) similarities (based on Euclidian distance) were compared to fish species similarities among surveys with the BEST procedure in the Primer 7 statistical program (Clarke et al. 2014). This procedure compares the species rank order similarities with the environmental rank order similarities and tests for significance (Spearman's rho, $P \leq 0.05$) from a statistical probability distribution derived from permutations of surveys (Clarke et al. 2014).

Mean lengths (TL mm) of the dominant species were compared among reef types, locations, and seasons with three-way ANOVA. All differences were considered significant at $P \leq 0.05$. If significant differences were detected with ANOVA or generalized linear models, specific differences were assessed with a Tukey post-hoc test (Zar 2010).

Results

Total Fish Densities

The density of the fish assemblage (all species combined) was higher on mid-shelf reefs compared to inner- or outer-shelf reefs (χ^2 = 9.2, P = 0.010) and higher in the fall compared to other seasons (χ^2 = 10.8, P = 0.013; Table 1). Fish density was also associated with an interaction of reef type and location, with higher densities on big reefs at mid-shelf locations compared to small reefs at outer-shelf locations and big reefs at inner-shelf locations (χ^2 = 15.5, P = 0.004; Table 2).

Individual Species

We identified 66 fish taxa (lowest taxa: 58 species, five genera, three families) from visual surveys on artificial reefs in the northern Gulf of Mexico. When examining reef attributes and affinities of the associated species, we removed Round Scad *Decapterus punctatus*. Even though it was the most abundant species (40.2%), it is generally considered a transient, pelagic species (McBride et al. 2002). After removal of Round Scad, the artificial reefs examined in the present study were dominated by Red Snapper (35.3%), Tomtate *Haemulon aurolineatum* (22.4%), Vermilion Snapper *Rhomboplites aurorubens* (19.5%), Atlantic Spadefish *Chaetodipterus faber* (7.0%), Greater Amberjack *Seriola dumerili* (3.0%) and Gray Triggerfish *Balistes capriscus* (1.8%). These six most abundant species comprised 89% of the total number of individuals (Table 1). Other common species (1.0–1.4%) on reefs included Cubbyu *Pareques umbrosus*, Gray Snapper *Lutjanus griseus*, lionfish *Pterois* spp., and Whitespotted Soapfish *Rypticus maculatus*.

There were significant differences in density associated with reef type, location, season, and interactions that depended on species. Tomtates had higher densities on tank and small reefs, at inner- and mid-shelf locations, and during summer and fall seasons. Vermilion Snapper had higher densities at mid- and outer-shelf locations, and during the fall. Atlantic Spadefish had higher densities at mid-shelf locations, and during the spring. Greater Amberjacks had higher densities during the fall (Table 1).

Vermilion Snapper had higher densities associated with interactions of big and tank reefs at inner-shelf locations. Greater Amberjacks had higher densities on big reefs at outer-shelf locations, compared to big reefs on inner-shelf locations (Table 2). Tomtates had higher densities associated with interactions of big reefs during the fall and with mid-shelf locations during the fall, and Atlantic Spadefish had higher densities associated with mid-shelf locations during the winter (Table 3).

Tomtates had higher densities associated with three-way interactions at big reefs at mid-shelf locations during the fall (χ^2 = 13.5, P = 0.019). Vermilion Snapper had higher densities associated with three-way interactions of big reefs at mid-shelf locations during the fall (χ^2 = 11.9, P = 0.036). Atlantic Spadefish had higher densities associated with three-way interactions for small reefs at mid-shelf locations during the winter (χ^2 = 17.6, P = 0.004).

Size Comparisons

Larger mean sizes (TL mm) were detected for Red Snapper and Greater Amberjack on big reefs, for Atlantic Spadefish on big and tank reefs, for Vermilion Snapper on tank reefs, and for Tomtate on small reefs (Table 4). Larger sizes were detected for Red Snapper, Atlantic Spadefish, and Greater Amberjack on outer-shelf locations; for Vermilion Snapper on outer- and mid-shelf locations; and for Tomtate on inner-shelf locations

Table 1. Mean and percent densities (number/100 m^2) for all fish and dominant fish species ($\geq$1.3% of the total density) for all surveys; and least-square mean densities by reef type, shelf location and season, on artificial habitats in the northern Gulf of Mexico for 2012–2015. Wi = winter, Sp = spring, Su = summer and Fa = fall. Different letters indicate significant ($P \leq 0.05$) differences within reef type, shelf location, and season.

			Reef type			Shelf location			Season			
Species	Mean	%	Big	Tank	Small	Inner	Mid	Outer	Wi	Sp	Su	Fa
All species			237	278	225	224 y	313 z	201 y	226 y	177 y	212 y	352 z
Red Snapper *Lutjanus campechanus*	98	35.3	85	105	84	97	95	79	64	91	97	92
Tomtate *Haemulon aurolineatum*	62	22.4	14 y	30 z	28 z	28 z	38 z	13 y	5 y	8 y	41 z	53 z
Vermilion Snapper *Rhomboplites aurorubens*	54	19.5	11	19	19	8 y	26 z	20 z	9 yx	3 x	13 y	82 z
Atlantic Spacefish *Chaetodipterus faber*	19	7.0	9	4	1	3 zy	5 z	2 y	3 xy	13 z	<1 x	4 y
Greater Amberjack *Seriola dumerili*	8	3.0	6	6	4	2	8	6		2 y	5 y	13 z
Gray Triggerfish *Balistes capriscus*	5	1.8	3	5	4	3	5	4	2	4	3	6

Table 2. Least-square mean density (number/100 m^2) for all species, Vermilion Snapper, and Greater Amberjack associated with an interaction of reef type and shelf location on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

		Reef type		
Species	Location	Big	Tank	Small
All species	Inner	167 yx	243 zx	274 zx
	Mid	522 z	253 zx	350 zy
	Outer	216 zx	397 zy	156 x
Vermilion Snapper	Inner	<1 w	1 xw	89 z
	Mid	119 z	38 zy	41 zy
	Outer	77 zy	121 z	10 yx
Greater Amberjack	Inner	3 yx		8 zy
	Mid	12 zy	12 zy	7 zx
	Outer	9 zx	21 z	3 yx

(Table 4). Seasonally, larger sizes were detected for Red Snapper in the winter and spring; for Tomtate, Vermilion Snapper, and Greater Amberjack in the spring; and for Atlantic Spadefish in the spring and summer (Table 4).

Several species were larger when associated with an interaction of reef type and shelf location. Red Snapper were larger on big reefs at outer-shelf locations, Tomtates on tank reefs at inner-shelf locations and small reefs at mid-shelf locations, Vermilion Snapper on tank reefs at inner- and mid-shelf locations and small reefs at outer-shelf locations, Atlantic Spadefish on big and tank reefs at mid-shelf locations, and Greater

Table 3. Least-square mean density (number/100 m^2) for Tomtate associated with an interaction of reef type and season, and for Tomtate and Atlantic Spadefish associated with an interaction of shelf location and season on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

		Season			
Species	Reef type	Winter	Spring	Summer	Fall
Tomtate	Big		12 xw	7 yxw	196 z
	Tank	1 w	11 xw	170 zy	82 zx
	Small	33 zw	89 zw	43 zw	53 zw
	Location	Winter	Spring	Summer	Fall
Tomtate	Inner	43 zx	27 yxw	43 zx	65 zx
	Mid	8 zw	6 xw	53 zx	213 z
	Outer		36 zw	82 zy	24 yxw
Atlantic Spadefish	Inner		13 yx	1 xv	6 yv
	Mid	531 z	22 y	1 wv	11 yxw
	Outer		29 yx	<1 v	6 yv

Table 4. Comparison of least square mean sizes ± SD (total length mm) within reef type, shelf location, and season for dominant species (>1.3% of the total density) on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

	Reef type			Shelf location			Season			
Species	Big	Tank	Small	Inner	Mid	Outer	Winter	Spring	Summer	Fall
Red Snapper	433	416	376	374	388	452	427	435	396	385
	±141 z	121 y	±157 x	±145 x	±132 y	145 z	±181 z	±142 z	±139 y	±134 x
Tomtate	121	62	158	145	121	71	117	208	91	115
	±78 y	±60 x	±70 z	±69 z	±83 y	±63 x	±38 y	±40 z	±76 x	±80 y
Vermilion Snapper	145	166	91	60	157	152	98	315	99	134
	±95 y	±124 z	±83 x	±47 y	±103 z	±115 z	±76 x	±37 z	±92 x	±105 y
Atlantic Spadefish	287	290	139	209	173	241	138	287	278	252
	±63 z	±46 z	±24 y	±67 y	±75 x	±63 z	±20 x	±52 z	±72 z	±84 y
Greater Amberjack	617	495	410	400	477	560		622	490	469
	±275 z	±157 y	±159 x	±179 x	±193 y	±218 z		±144 z	±172 y	±228 y

Amberjacks on big reefs at outer-shelf locations (Table 5).

Several species were larger when associated with an interaction of reef type and season. Red Snapper were larger on big reefs during the fall and on big and tank reefs during the winter, Vermilion Snapper on tank reefs during the winter and spring, Atlantic Spadefish on big and tank reefs during the spring and tank and small reefs during the summer, and Greater Amberjacks on big reefs during the spring and fall (Table 6).

Several species were larger when associated with an interaction of shelf location and season. Red Snapper were larger at outer-shelf locations during the winter and spring, Tomtates at mid-shelf locations during the spring, Vermilion Snapper at outer-shelf locations during the winter and inner- and at mid-shelf locations during the spring, Atlantic Spadefish at outer- and inner-shelf locations during the summer and at mid-shelf during the spring and fall, and Greater Amberjacks at inner- and mid-shelf reefs during the spring (Table 7).

Also, there were larger fish associated with three-way interactions. Red Snapper were larger on big reefs at outer-shelf locations during the winter ($F_{5,\ 8334} = 27.5$, $P < 0.001$). Tomtates were larger on big reefs at mid-shelf locations during the summer ($F_{2,\ 5585} = 10.2$, $P < 0.001$). Vermilion Snapper were larger on tank reefs at outer-shelf locations during the winter ($F_{1,\ 5279} = 34.8$, $P < 0.001$). Atlantic Spadefish were larger on small reefs at inner-shelf locations during the spring and on tank reefs at outer-shelf locations during the summer ($F_{1,\ 1753} = 148$, $P < 0.001$). Greater Amberjacks were larger on big reefs at outer-shelf locations during the fall ($F_{3,\ 745} = 25.9$, $P < 0.001$).

Table 5. Least square mean sizes (Total length mm) for dominant species (>1.3% of the total density) associated with an interaction of reef type and shelf location on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

		Reef type		
Species	Location	Big	Tank	Small
Red Snapper	Inner	396 x	446 y	308 u
	Mid	435 y	374 w	353 v
	Outer	504 z	448 y	438 y
Tomtate	Inner	174 y	205 zy	136 x
	Mid	122 w	62 v	203 z
	Outer	46 v	54 x	145 x
Vermilion Snapper	Inner	241 zywv	267 zyx	59 v
	Mid	127 w	253 z	133 xw
	Outer	176 y	128 w	231 z
Atlantic Spadefish	Inner	260 yx	246 xw	156 u
	Mid	307 z	303 z	138 t
	Outer	232 w	281 y	185 v
Greater Amberjack	Inner	274 v		435 w
	Mid	550 y	532 y	300 v
	Outer	813 z	468 xw	542 yx

Table 6. Least square mean sizes (total length mm) for dominant species (>1.3% of the total density) associated with an interaction of reef type and season on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

		Season			
Species	Reef type	Winter	Spring	Summer	Fall
Red Snapper	Big	452 zy	471 z	338 u	453 z
	Tank	470 z	415 yxw	422 yx	389 v
	Small	390 wv	378 wvu	406 xv	339 u
Tomtate	Big		210 zy	237 zy	114 v
	Tank	241 zxwvut	228 z	43 t	64 u
	Small	117 v	190 yx	155 w	176 x
Vermilion Snapper	Big		306 y	289 zy	136 w
	Tank	379 z	323 zy	79 u	172 x
	Small	79 u		108 v	87 u
Atlantic Spadefish	Big		293 z		280 y
	Tank		304 z	278 zy	271 y
	Small	138 w	173 x	280 zy	159 x
Greater Amberjack	Big		698 z	391 wv	631 zy
	Tank		565 yx	513 xw	461 w
	Small			505 xw	342 v

Table 7. Least square mean sizes (total length mm) for dominant species (>1.3% of the total density) associated with an interaction of shelf location and season on artificial habitats in the northern Gulf of Mexico for 2012–2015. Different letters indicate significant differences ($P \leq 0.05$) within species.

		Season			
Species	Reef type	Winter	Spring	Summer	Fall
Red Snapper	Inner	391 w	437 yx	318 v	333 v
	Mid	241 u	420 x	376 w	379 w
	Outer	517 z	488 z	449 y	426 x
Tomtate	Inner	116 v	211 y	130 wv	137 w
	Mid	134 xwv	252 z	138 w	116 v
	Outer		170 x	63 u	77 u
Vermilion Snapper	Inner	77 u	267 zyxw	43 t	50 t
	Mid	140 xwvu	335 zy	111 v	163 x
	Outer	379 z	305 y	101 v	149 w
Atlantic Spadefish	Inner		258 y	280 zyx	147 w
	Mid	138 w	311 z	265 y	303 z
	Outer		247 yx	343 z	232 x
Greater Amberjack	Inner		597 zyxw	504 yx	326 w
	Mid		670 z	386 xw	430 x
	Outer		564 y	539 y	571 y

Richness, Evenness, and Diversity

Richness ($F_{2,58} = 6.1$, $P = 0.004$) and Shannon–Wiener diversity ($F_{2,58} = 7.0$, $P = 0.002$) indices were higher on tank and big reefs (Figure 3). Richness was lower during the winter ($F_{3,58} = 5.4$, $P = 0.003$), evenness was lower during the winter ($F_{3,58} = 5.7$, $P = 0.002$), and Shannon–Wiener diversity was higher during the fall and lower during the winter ($F_{3,58} = 9.5$, $P < 0.001$; Figure 4). No significant interactions were associated with reef type, shelf-location, or season for richness, evenness, or diversity indices.

Fish Communities

Three-way PERMANOVA analysis indicated differences in fish assemblages relative to reef type (pseudo-$F_{2,58} = 2.8$, $P = 0.001$), location (pseudo-$F_{2,58} = 3.3$, $P = 0.001$), and season (pseudo-$F_{2,58} = 2.0$, $P = 0.007$). Pairwise tests showed specific differences (Table 8). Visual examination of the MDS plot indicates differentiation of small reefs from big and tank reefs (Figure 5) but little separation for shelf locations or seasons (not shown).

Temperature, salinity, and dissolved oxygen were similar among shelf locations (Figure 6). Salinity was also similar over seasons, temperatures were lowest in winter, and dissolved oxygen had minimum levels in late summer but never dropped below 3 mg/L (Figure 6). Abiotic factors (temperature, salinity, dissolved oxygen, and depth) had no significant effect on the fish assemblage for any single or combinations of environmental variables (Spearman's Rho = 0.117, $P = 0.076$).

Discussion

Diversity Measures

Reef fish diversity measures in the present study were significantly associated with all three main reef attributes or factors: reef type, shelf location, and season. It was not surprising that higher assemblage diversity was observed at big and tank reefs in comparison to small reefs as these diversity to habitat size relations reflect classical species area patterns well documented in the literature (Molles 1978; Sale and Douglas 1984; Schroeder 1987; Bohnsack et al. 1994; Chittaro 2002; Jordan et al. 2005). Clearly, larger reefs (e.g., ships or army tanks) provide greater vertical relief that can attract more upper water column species, more stable structure that allows for species that tend to borrow under structures (many Serranidae and Lutjanidae), and perhaps more shelter habitat for smaller species to avoid predators. Further, assemblage diversity relations documented here align with the time-stability hypothesis where the big and tank artificial reefs were older and served as a reef for longer time periods to attract and retain more species and individuals (Hessler and Sanders 1967; Sanders 1968; McClain and Schlacher 2015).

When compared to open habitat, it is generally accepted that artificial reefs will increase numbers of individuals and species diversity compared to natural sand-mud habitat in marine shelf habitats (Bohnsack 1989; Milon 1989; Fabi and Fiorentini 1994; Mills et al. 2017). Although not tested in the present study (open habitats were not sampled), previous comparisons of reef complexity among artificial habitats confirm such patterns in the northern Gulf of Mexico (Lingo and Szedlmayer 2006). In addition to structural complexity, these patterns may also be related to increased epifaunal communities that provide increased forage base associated with artificial reefs (Hueckel and Buckley 1987; Redman and Szedlmayer 2009).

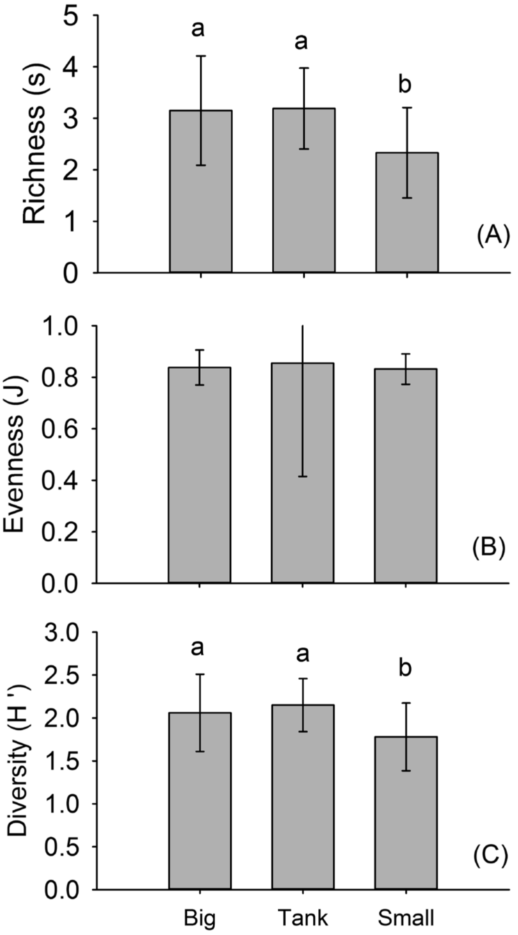

Figure 3. Comparison of diversity indices by reef type. **(A)** Species richness, **(B)** evenness, and **(C)** Shannon–Wiener diversity. Significant differences (P < 0.05) are indicated by different letters.

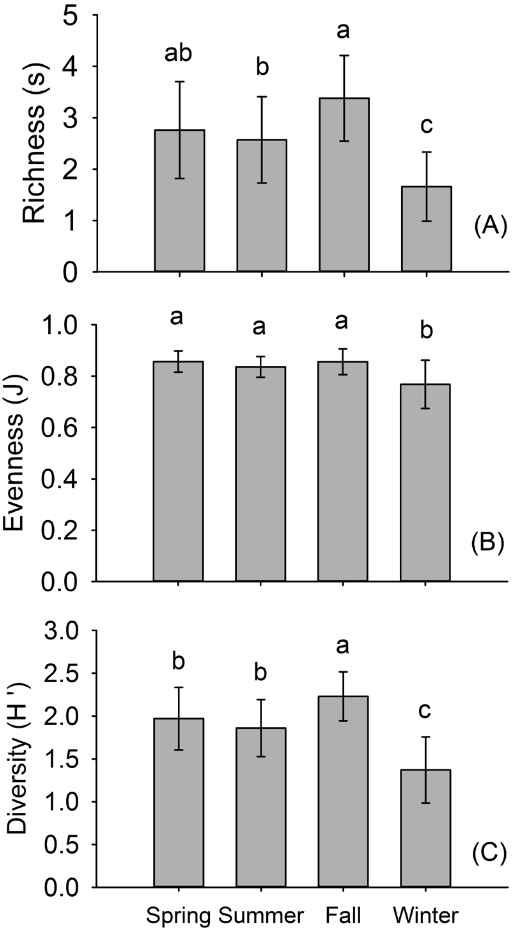

Figure 4. Comparison of diversity indices by season. **(A)** Species richness, **(B)** evenness, and **(C)** Shannon–Wiener diversity. Significant differences (*P* < 0.05) are indicated by different letters.

It was also expected that diversity would be greater during the fall. Again, this is a pattern that has been well documented in previous studies of artificial reef fish assemblages that showed seasonal changes on both large and small oil platforms (<4 m^3) reefs in the northern Gulf of Mexico (Stanley and Wilson 1991; Lingo and Szedlmayer 2006; Redman and Szedlmayer 2009). The increase in fish assemblage diversity during the fall is most likely related to increased water temperature, which facilitates an increase in tropical recruits (usually not observed at other times of the year). This temperature increase also aids the reef colonization of age-0 recruits of many reef fish species with more temperate and tropical affinities that spawn in the spring and summer and move to reef structure in the fall (Rooker et al. 1997; Szedlmayer and Conti 1999; Szedlmayer and Lee 2004; Hernandez et al. 2010; Szedlmayer 2011).

Table 8. Fish assemblage comparisons based on Bray–Curtis similarity by reef type, shelf location, and season from April 2012 to November 2015. Significant ($P \leq 0.05$) differences are indicated (*) for pairwise comparisons after significant effects were detected with three-way PERMANOVA. Only main effects are shown, as all two-way and three-way interactions were not significant.

Reef type	Pseudo-*t*	Exact *P*
Big, small	1.8	0.003*
Big, tank	0.6	0.936
Small, tank	2.0	0.001*
Shelf location		
Inner, mid	1.3	0.077
Mid, outer	1.8	0.004*
Inner, outer	2.0	0.001*
Season		
Fall, spring	1.8	0.002*
Fall, winter	1.6	0.014*
Fall, summer	1.1	0.256
Spring, winter	No test	
Spring, summer	1.1	0.272
Winter, summer	1.5	0.034*

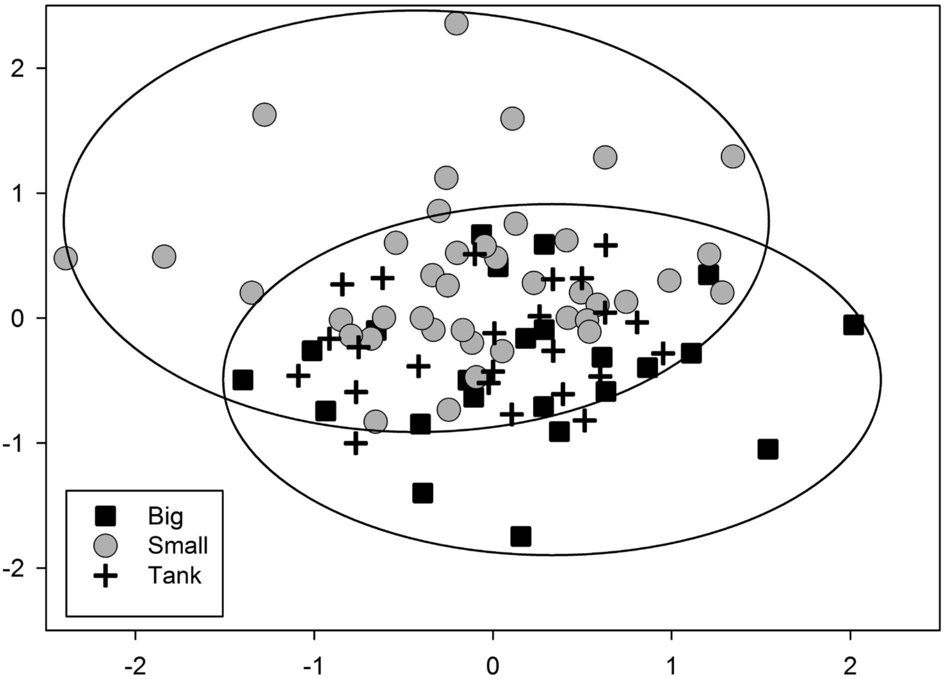

Figure 5. Ordination plot (multidimensional scaling) of fish assemblages based on Bray–Curtis similarity coefficients by reef type. Big reefs = squares, tank reefs = crosses, and small reefs = gray circles.

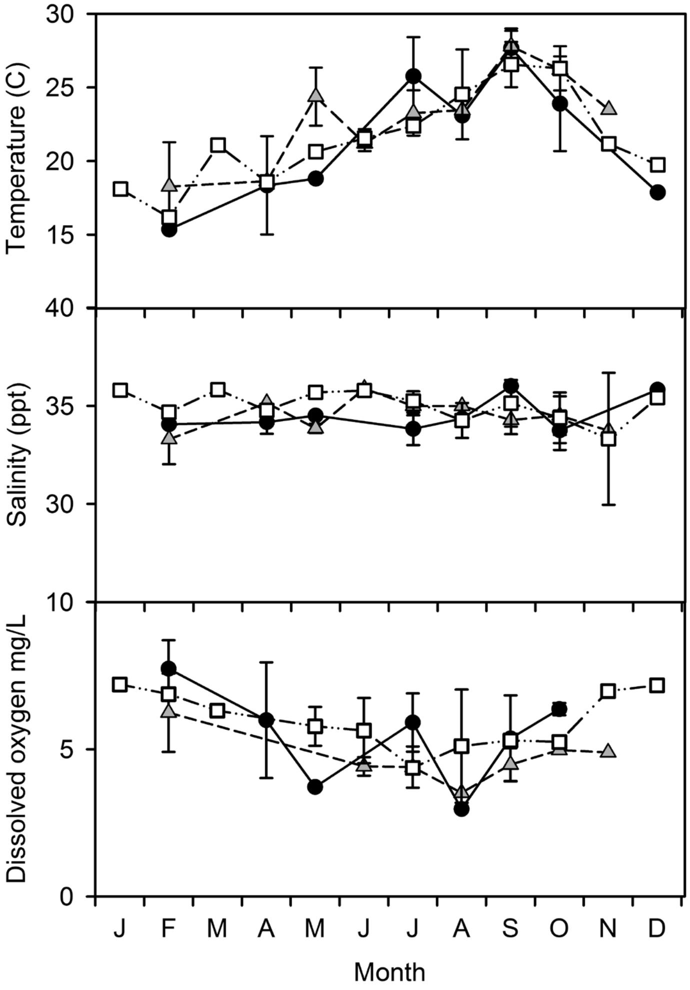

Figure 6. Mean ± SD temperature (°C), salinity (‰), and dissolved oxygen (mg/L) by shelf location and month from 2012 to 2015. Black dots with solid line = inner shelf, gray triangles with dashed lines = mid shelf, and open squares with dash-dot lines = outer shelf. Error bars = SD.

Fish Community Similarity Comparisons

Faunal similarity (i.e., Bray–Curtis similarity index) based on fish assemblage composition was similar to the assemblage diversity measures with regard to associations it had with reef attributes such as reef type, location, and season. Additionally, there were no interaction effects detected among the reef attributes relative to faunal similarity. Assemblage similarity identified groups associated with big and tank reefs as differing from small reefs, as with diversity measures. In the present study, tank reefs might be considered more similar to big reefs than small reefs in that tank reefs were large enough to attract and retain larger reef fishes. Also, as previously stated, longevity of big and tank reefs likely caused similarity differences from small reefs. For example, the northern Gulf of Mexico is subject to regular disruption from major tropical storms. These storms not only affect coastal areas, but large waves (>6 m) can reach the continental shelf sea floor (Wang et al. 2005) and may destroy smaller and generally more fragile reef structures or cause artificial reefs to subside and become buried in the substrate. Thus, small reefs (metal cages, sunken boats, concrete pyramids, etc.) might be expected to persist for shorter time periods while big and tank reefs are more permanent structures and fish communities can attain maximum carrying capacities due to longer reef existence. Further, confirmation of reef longevity is shown in the present study where tank reefs were still present and structurally intact 21 years after deployment. Similar conclusions were observed for fish communities on artificial reefs off Pensacola, Florida, where the decrease in larger piscivores (Serranidae) were associated with the reduction in smaller concrete artificial reefs, which were apparently became buried during tropical storms (Dance et al. 2011).

Another aspect of artificial reef fishes that became apparent in the present study was the differences among assemblages on outer-shelf locations from those on the mid- and inner-shelf locations. This pattern was consistent with the effect of reef type on fish communities and can be similarly explained with more consistent temperature, salinities, and structure longevity (deeper artificial reefs are less prone to wave action; i.e., greater stability). In addition, fish species that tend to occur in deeper water have a greater potential for contributing to fish diversity on the outer shelf due to the closer proximity of the extensive mesophotic deep reefs on the continental slope (Weaver et al. 2001; Beyea and Szedlmayer 2016). Similar patterns were observed off the Texas coast, where similarities in fish assemblages were related to depth (Ajemian et al. 2015). However, it is difficult to compare the Texas study to the present study because in that study, all reefs examined were deeper (34–84 m, similar to the outer-shelf locations in the present study) and all of reef types investigated were oil-gas platforms and classified as big reefs in the present study.

Total Fish Densities

Fish densities were greater on reefs at mid-shelf locations. This observation may be explained by the greater densities of unpublished small reefs inside the artificial reef permit zones on this part of the shelf (S. T. Szedlmayer and P. A. Mudrak, unpublished side-scan sonar surveys). Off coastal Alabama, artificial reef building started in 1953 with the deployment of 250 automobile bodies, and additional automobiles continued to be added at a steady rate for the next 30 years. Subsequently, reef building in the area substantially increased with the official designation of the Hugh Swingle General Permit Area in 1991 (Tatum 1993; Minton and Heath 1998). This mid-shelf reef building area has been in place for more than 60 years, and it is likely that its proximity to coastal ports has allowed fishers to deploy more artificial reefs in this area compared to other reef-building permit areas further offshore. Similar to assemblage diversity, total fish densities were greater in the fall, and as previously stated are most likely related to new age-0 recruits. However, there is a high mortality among these age-0 recruits during their first few months on the reef structure. Subsequently, their density will precipitously decline in the winter and spring (Szedlmayer 2011).

It is speculated that natural reefs in deeper waters on the continental slope should have higher diversity when compared to any shelf location examined in the present study. In fact, there is evidence that assemblages at these extensive offshore natural rock pinnacles have a higher species richness (113 fish species identified, Weaver et al. 2001). Oppositely, the population densities were lower on these deep reefs as fish were spread out over hundreds of meters of natural rocky habitat as opposed to being concentrated at a relatively small artificial reefs surveyed in the present shelf study.

Comparisons across the Northern Gulf of Mexico

Reef fish assemblages observed in the present study were similar to assemblages observed in a northwest Florida study in an adjacent area immediately east of the present study site (Dance et al. 2011). In both studies, Red Snapper and Tomtate were the dominant species. The top 10 species were also similar between the two studies, with the exception that Pinfish *Lagodon rhomboides* and Jackknifefish *Equetus lanceolatus* comprised 6–7% of the assemblage off Florida but represented less than 0.001% of the individuals observed in the present study. Although Red Snapper and Gray Triggerfish were dominant species off Alabama and northwest Florida, they did not display any preferences for artificial reef factors (reef type, location, and season) examined in the present study. Thus, community patterns were driven by other species (e.g., Tomtate, Vermilion Snapper, Atlantic Spadefish, and Greater Amberjack). Each of these species had different associations for main and interaction effects and none with the same associations for reef type, location, or season.

Comparisons to other artificial reef fish assemblages at greater distances from the present study (e.g., off Louisiana, Texas, and central Florida) had greater differences from the present study, with species differences ranging from 40% to 85% (Smith et al. 1979; Rooker et al. 1997; Wilson et al. 2003; Ajemian et al. 2015), and these differences were most likely attributed to geographical separation (Floeter et al. 2008). Consistent with greater differences in dominant fish species with increasing distance from the present study are changes in substrate type, with the Florida shelf showing more sand and rock rubble habitat, the Alabama shelf with greater sand-mud substrate, and the western shelf off Louisiana and Texas showing more mud-silt substrate (Dufrene 2005; Jenkins et al. 2008; Williams et al. 2012). This suggests that the changing fish compositions on artificial reefs across the northern Gulf of Mexico were related to these changing substrate types.

Fish Size Comparisons

Size (TL mm) of dominant species (>1.3 of the total density) was significantly different with regard to reef type, location, season, and two-way and three-way interactions, but the relations were inconsistent among species. Larger Red Snapper, Atlantic Spadefish, and Greater Amberjacks were associated with big and tank reefs, the outer-shelf location, and the spring season. These observations are similar to previous studies that suggested an ontogenetic habitat shift with age and size. For example, Red Snapper initially settle on the inner shelf on small reefs, and as they grow older and larger, they move to increasingly larger reefs (Gallaway et al. 2009; Jaxion-Harm and Szedlmayer 2012). These observations are further reinforced by the indication that there was a significant interactive effect between reef type and shelf location, with the smaller fish associated with small reefs at inner-shelf locations and larger fish associated with big reefs at outer-shelf locations. However, fishing mortality for Red Snapper and Greater Amberjacks could also explain the presence of larger-sized fish at outer-shelf locations. Artificial reefs that are closer inshore would be expected to experience higher fishing mortality rates, and removal of larger-sized fish on the inner shelf would result in similar distributional patterns (Gordon 1993; Kanamoto 1996). In contrast, we would not expect that fishing mortality would play a role for Atlantic Spadefish population dynamics as this species is not typically targeted by fishers or any part of the bycatch of any particular fishery.

Vermilion Snapper size (TL mm) associations with reef attributes most likely reflect an ontogenetic habitat shift as smaller fish occurred on small reefs at inner-shelf locations. These fish apparently moved to other reef types and locations as they matured. Atlantic Spadefish occurred at a larger size on big and tank reefs, but based on two-way interactions, these larger fish were also associated with mid-shelf locations. For these two species, the presence of larger fish on larger reefs likely resulted from predation pressure and habitat suitability, with little influence from fishing mortality.

The size of Tomtate, the second most dominant species, can be attributed to predation pressure alone. The smallest Tomtates were observed on big reefs at outer-shelf locations, and this coincided with the presence of larger Red Snapper and Greater Amberjacks on big reefs at outer-shelf locations. Also, the smallest Tomtates were observed during the summer. This seasonal occurrence likely resulted from a substantial increase in the number of age-0 fish on these reefs in late summer. This species was the smallest of any species associated with artificial reefs in the present study. It was likely that they were present on the reefs earlier as newly metamorphosed juveniles (<25 mm TL) in July, but unfortunately, these fish were too small for valid visual identification. Only after these new recruits grew larger and were repeatedly observed in later surveys were they identified as Tomtates. Tomtate is a confirmed prey for Red Snapper (Wells et al. 2008; Szedlmayer and Brewton, unpublished data) and most likely consumed by Greater Amberjack as well. We suggest that larger predators occurring on the big reefs at outer-shelf locations consumed Tomtate when it attained an optimum prey size, which resulted in smaller Tomtate on these reefs.

Conclusions

Fish assemblages associated with artificial reefs in the northern Gulf of Mexico displayed substantial differences in their habitat affinities or preferences. These differences were significantly associated with reef types, shelf locations, and seasons. In the present study, fish assemblages associated with big reefs (e.g., ships) were more similar to assemblages associated with tank reefs (i.e., U.S. Army tanks) when compared to assemblages associated with small reefs (e.g., metal cages and concreate pyramids). The larger size, longer life span, and relative stability of the big and tank reefs were most likely the drivers of these fish assemblage observations. Similarly, more stable conditions in greater depths (less affected by tropical storms) and proximity to deepwater reefs (pinnacles), and their distinctive associated fauna on the continental slope may have contributed to the increased diversity on the artificial reefs located on the outer shelf. As in previous studies, species diversity and number of individuals were highest during the fall as there was an increase in recruitment from more tropical species and new age-0 recruits that were spawned that same year. Geographically, the highest fish density occurred on reefs at mid-shelf locations. This higher density was most likely due to a combination of a higher number of artificial reefs and reduced fishing pressure in comparison to assemblages associated with inner-shelf locations. In general, artificial reefs have added significantly to both the diversity and abundance of reef-associated fish assemblages on the continental shelf off the coast of Alabama and most likely elsewhere in the northern Gulf of Mexico. However, not all artificial reefs are the same. Consequently, when artificial reefs are used by resource managers to help restore fish populations, it is important that they consider reef type, location, and survey season in their assemblage assessments. Also, individual target species may influence other assemblage members, and considerations should be made as to the overall objectives (faunal diversity, population abundance, species fitness) when proposing artificial reef deployments.

Acknowledgments

We thank M. Albins, R. Brewton, L. Grove, J. Herbig, D. Horn, C. Roberts, and J. Williams-Grove for assistance in the field and laboratory. This manuscript is a contribution of the Alabama Agricultural Experiments Station and the School of Fisheries, Aquaculture and Aquatic Sciences, Auburn University, and was supported by the Natural Resource Damages & Regulatory Affairs, Gulf Coast Restoration Organization, BP America Inc. (grant number GCRO-TX-9039).

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