

Reef fish assemblages differ both compositionally and functionally on artificial and natural reefs in the eastern Gulf of Mexico

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Abstract

Human-made structures, particularly artificial reefs, have played an increasingly important role in restoration, conservation, and management efforts aimed at mitigating the detrimental effects of anthropogenic activities on habitats and their associated communities. However, the extent to which artificial reefs support marine assemblages resembling those of natural habitat remains unclear. In this study, we used a 10-year dataset of reef fish visual surveys performed on paired reefs located in the eastern Gulf of Mexico, complemented by functional trait data, to examine whether artificial and natural reefs support fish assemblages with similar taxonomic and functional diversities. Our results revealed compositionally and functionally distinct assemblages between reef types, a pattern that was consistent across depths. The inclusion of functional diversity allowed us to explicitly identify generalized patterns in the composition of these assemblages that may have only been inferred from a strictly taxonomic-based approach. Specifically, large-bodied, midwater predators were relatively more abundant on artificial reefs, whereas smaller-bodied, benthic-associated invertivores or mesopredators were more frequently observed on natural reefs. The artificial reefs in this study were previously characterized as having greater vertical relief than their natural counterparts, a feature that likely contributed to the greater abundances of midwater predators on those reefs. Similarly, natural reefs typically offered a greater abundance of medium-to-small refugia necessary for smaller-bodied taxa to forage and avoid predation. Previous work also demonstrated that these artificial reefs were visited 2-10 times more frequently by boaters than natural reefs, presumably for recreational fishing purposes. These findings led us to infer that local-scale environmental filtering and variable predator-prey dynamics resulting from differences in the physical characteristics of these reefs coupled with asymmetric fishing activity influenced the observed differences among reef fish assemblages. Additionally, our work underscored the utility of multiple diversity measures in comparative assemblage studies, provided insight into reef-fish assemblage dynamics, and helped to emphasize a pressing need to better understand the role of human-made structures in marine ecosystems.

Keywords: community dynamics; assembly patterns; fisheries ecology; time series; community-weighted means

Introduction

Globally, anthropogenic activities have resulted in the alteration of habitats and their associated communities (e.g. Fodrie et al. 2010, Wilson et al. 2010, Bates et al. 2013, Blowes et al. 2019, Purtlebaugh et al. 2020, Gotelli et al. 2021, Stuart-Smith et al. 2021). The disruption of these natural systems has warranted mitigation, restoration, or management efforts that promote continued and sustainable access to ecosystem services. Human-made structures have become a major component of those efforts (Lima et al. 2020). In fact, the deliberate use of human-made materials to establish new or restored habitat has occurred in marine systems for decades (i.e. artificial reefs; Lindberg and Seaman 2011, Becker et al. 2018), and recent estimates suggest an increased use of artificial reefs worldwide (Lima et al. 2019). However, it remains unclear whether artificial reefs support marine assemblages similar to those of natural reefs (e.g. Carr and Hixon 1997, Simon et al. 2013, Granneman and Steele 2015, Paxton et al. 2020a). Additional research on assemblage patterns across various forms of marine habitat will help to improve our understanding of these systems and has the potential to provide information that may help to guide future restoration, conservation, and management efforts.

The influence of structural complexity and habitat connectivity on assembly patterns has been extensively documented in marine systems (e.g. Rilov and Benavahu 2000, Gratwicke and Speight 2005, Strain et al. 2021). For example, there are a variety of breakwater structures and offshore petroleum platforms that support diverse marine assemblages and facilitate increased population connectivity in addition to their intended maritime and economic functions (Burt et al. 2013, Claisse et al. 2014, Scyphers et al. 2015, Mclean et al. 2022). In contrast, artificial reefs are used to enhance fisheries production, support ecotourism, rehabilitate habitat, or contribute to the preservation of biodiversity (Lee et al. 2018, Lima et al. 2019, Paxton et al. 2020a). Although some evidence would suggest that artificial reefs successfully achieve these diverse objectives, many of those studies were based on data collected over a duration of 2 years or less (Lima et al. 2019). Similarly, Paxton et al. (2020a) demonstrated that although

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Table 1. Description	of the	study	reefs
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	Reef name	Reef type	Reef material(s)	Year deployed	Depth (m)	Max vertical relief (m)	Surveys per PSU (mean ± se)
Shallow	Clearwater Reef	Artificial	Concrete culverts, bridge pilings, and a barge	1974–99	9	4.0	3.08 ± 0.19
	21HS	Natural	Meandering limestone ledge	-	10	2.0	3.18 ± 0.17
	St. Pete Beach Reef	Artificial	Concrete culverts, 10 steel army tanks, and a 60 m barge	1984–95	12	4.0	3.21 ± 0.17
	AC5	Natural	Limestone escarpment	-	14	<1.0	3.31 ± 0.20
Deep	Pinellas II Caves	Artificial Natural	Two 55 m steel-hull ships Limestone escarpment	1982 -	24 25	11.0 1.5	3.21 ± 0.20 3.21 ± 0.20
	Treasure Island II Florida Fishermen's Ledge	Artificial Natural	26 m steel-hull ship Meandering limestone ledge	2004 _	30 27	12.0 <1.0	$\begin{array}{c} 3.26 \pm 0.19 \\ 3.33 \pm 0.18 \end{array}$

Note: Reef material(s), year deployed, and vertical relief were based on the values reported in Wall and Stallings (2018)

artificial reefs can support assemblages comparable to natural reefs, fish biodiversity can also be highly variable among artificial reefs. They also have the potential to negatively affect biodiversity through the homogenization of regional communities (Dafforn et al. 2015) or an increased prevalence of invasive species (Airoldi et al. 2015). Additional studies that compare assemblage patterns among artificial and natural reefs (e.g. Carr and Hixon 1997, Streich et al. 2017, Garner et al. 2019), particularly those based on long-term data, are therefore essential for a more comprehensive understanding of the role of artificial reefs in the management of marine ecosystems.

One frequently overlooked aspect of comparative reef studies is whether variations in species composition and abundance among assemblages manifest as differences in the functional diversity of those assemblages. In other words, how do certain species affect the representation of various morphological forms or ecological guilds within an assemblage? Functional diversity data are typically less complex than taxonomic composition and abundance data (Parravicini et al. 2020) and may help to identify processes that structure assemblages (Mouchet et al. 2010, Leibold and Chase 2018). For example, if artificial and natural reefs support compositionally distinct assemblages but those taxa exhibit similar functional characteristics, then we might infer that interactive processes such as competition or niche filtering limit the coexistence of otherwise functionally similar taxa. In contrast, if those same compositionally distinct assemblages exhibit differences in their functional diversity, it may be reasonable to infer that non-interactive processes affect assembly patterns, such as dispersal or local-scale habitat filtering. Consequently, comparative studies may benefit from estimates of functional diversity to gain additional insight into potential processes that structure those assemblages (Mouchet et al. 2010).

The placement of artificial reefs in marine systems is often influenced by various stakeholder objectives and frequently results in spatial separation from existing natural reefs to mitigate unintended negative effects. This presents a challenge when developing comparative studies that account for spatially variable factors which could influence assembly patterns, such as depth or larval supply (*sensu* Carr and Hixon 1997, Granneman and Steele 2015). However, the eastern Gulf of Mexico offers a suitable model study system due to the widespread presence of artificial reefs throughout the coastal shelf (Lima et al. 2019, Schulze et al. 2020, Gardner et al. 2022). In this study, we used a 10-year visual survey dataset of reef fish composition and abundance collected from spatially paired reefs located in the eastern Gulf of Mexico, complemented by functional trait data, to address the following two questions: (1) Do artificial and natural reefs support compositionally similar reef fish assemblages? (2) Do those assemblages exhibit similar trait-based functional diversity? Through the concurrent evaluation of both the compositionand trait-based diversity of these assemblages, we sought to improve our understanding of the processes that may influence reef fish assembly patterns on artificial and natural reefs in this system.

Methods

Study design and data collection

We performed seasonal (i.e. quarterly) underwater visual surveys while on SCUBA that quantified reef fishes at four pairs of artificial and natural reefs in the eastern Gulf of Mexico from 2013 to 2022 (Table 1, Fig. 1). Reefs within each pair were located near each other (8.1 \pm 2.4 km separation; mean \pm se) to control for the effects of abiotic (e.g. depth, temperature), biotic (e.g. larval supply, basal resources), and socioeconomic factors (e.g. access by fishers). Two reef pairs were located 9.6 \pm 1.6 km from shore at a depth of 11.3 ± 1.1 m (hereafter "shallow" reefs), and the other two reef pairs were 39.0 \pm 3.5 km from shore at a depth of 26.5 ± 1.3 m (hereafter "deep" reefs; Simard et al. 2016, Wall and Stallings 2018). We performed 10-minute stationary visual surveys on each reef during each season within each year (n = 2-4 surveys per reef each season each year; Table 1). For each survey, we identified (usually to species) and enumerated all fishes observed within an area determined by the lesser of two radii: 7.5 m, the maximum survey radius reported by Bohnsack and Bannerot (1986), or the estimated horizontal visibility during the survey $(5.2 \pm 0.1 \text{ m among all surveys})$. All surveys required a minimum horizontal visibility of 3.0 m.



Figure 1. Map of paired artificial and natural study reefs.

When *in situ* species-level identifications were impractical, we identified fishes to genus or family.

We typically required two single-day trips each season to complete surveys at all eight reefs, with two artificial-natural pairs (i.e. four reefs) surveyed per trip. Our goal was to ensure a high degree of temporal concordance among the surveys conducted within each season, every year. Therefore, we made efforts to minimize the time between day trips, within logistical constraints (e.g. diver availability, weather conditions, and COVID-19 pandemic). We did not target specific portions of a reef for surveys, although recreational fishing activity often influenced the structure(s) that we could safely dive during each visit. Additionally, SCUBA divers haphazardly chose the location of each visual survey within a reef in situ, and these surveys typically occurred within tens of meters of a central dive marker, dependent upon the reef's layout. The spatial extent of each reef allowed us to perform concurrent surveys with minimal overlap while also avoiding an excessive proportion of non-reef habitat (i.e. sand flat) within each survey.

Data preparation

We estimated taxon densities $(no./m^2)$ for the individual surveys performed on a reef during each season within each year. We then calculated mean taxon densities across those individual surveys to address their spatiotemporal nonindependence. This resulted in a single sample of mean taxon densities for each reef during each season within each year, henceforth referred to as the primary sampling unit (PSU). We chose to retain only those taxa present in at least 5% of PSUs to mitigate the effects of rare taxa (McCune et al. 2002). We applied this threshold to shallow- and deep-reef PSUs independently to prevent the erroneous exclusion of any taxa. For example, large-bodied pelagic fishes are relatively uncommon among shallow coastal habitats (Menezes et al. 2006, Brokovich et al. 2008, Stefanoudis et al. 2019). Such a taxon may have therefore fallen below the 5% threshold due to a preponderance of absences on shallow reefs if percent presence was based on all PSUs. Last, we used shade plots (Clarke et al. 2014) to visually inspect the effects of three different transformations commonly applied to composition and abundance data: square-, cube- and fourth-root (Fig. S1). We determined that a fourth-root transformation was necessary to sufficiently upweight rare taxa while simultaneously downweighting the highly abundant taxa that may have otherwise numerically dominated and biased analytical results (Anderson et al. 2006).

In addition to reef fish densities, we used the *rfishbase* package (Boettiger et al. 2019) in R (R Core Team 2023) to compile data from FishBase (Froese and Pauly 2023) on seven functional traits for each of the observed taxa. These data included three quantitative and four qualitative traits (Table 2), and we chose those traits because they are known to reflect the general ecology and habitat associations of most fishes (Mouillot et al. 2007, Bates et al. 2013, Stuart-Smith et al. 2013, Pecuchet et al. 2016). For example, fishes that engage in prolonged periods of swimming and cover large distances typically exhibit higher

Table 2. Functional trait list.

Trait	Туре	Category	Value(s)
Length _{max}	Quantitative	Diet and habitat use	Maximum reported total length (cm)
Trophic position	Quantitative	Diet	Diet-based trophic position (unitless)
Caudal fin aspect ratio	Quantitative	Habitat use and activity	Height ² -to-surface-area ratio of caudal fin (unitless)
Mouth position	Qualitative	Diet and habitat use	Superior, terminal, subterminal, inferior, other
Lateral profile	Qualitative	Habitat use and activity	Fusiform, elongated, eel-like, deep, other
Cross-sectional profile	Qualitative	Habitat use and activity	Angular, circular, compressed, oval, flattened
Preferred substrate	Qualitative	Habitat use	Hard, soft, mixed

Note: Trait type, how those traits described the observed taxon, and the units or classifications by which those traits were measured or defined. Traits were selected following Mouillot et al. (2007), Bates et al. (2013), Stuart-Smith et al. (2013), and Pecuchet et al. (2016). Also, see Pauly (1989a), Froese et al. (2010), Marenkov (2018), and Beukhof et al. (2019) for additional details and examples of the different morphological trait classifications.

caudal fin aspect ratios and streamlined bodies, whereas fishes that require precise maneuverability for foraging or predator avoidance often have lower caudal fin aspect ratios and less streamlined body shapes (Webb 1984, 1988). When specieslevel trait data were not available from FishBase, we approximated trait values based on related taxa (e.g. congeners) found in the Gulf of Mexico or western Atlantic. Specifically, we calculated an average value among related taxa for quantitative traits, whereas we selected the most frequently represented classification for the qualitative traits. We then consulted primary source texts, functional-trait database curators, and field guides to corroborate those approximations and to fill any data gaps that remained (e.g. McEachran and Fechhelm 1998, 2005, Bates et al. 2013, Stuart-Smith et al. 2013, Parravicini et al. 2020).

We used the *FD* package (Laliberté and Legendre 2010, Laliberté et al. 2014) in R to calculate community-weighted means for each trait in each PSU based on the equation

$$CWM_{i,j} = \sum_{k=1}^{n} p_{j,k} x_{i,k}$$

where $CWM_{i,j}$ is the community-weighted mean of trait *i* for PSU *j*, *n* is the number of taxa in PSU *j*, *p*_{*j*,*k*} is the relative fourth-root transformed density of taxon *k* in PSU *j*, and *x*_{*i*,*k*} is the trait *i* value for taxon *k* (Laliberté and Legendre 2010, Duarte et al. 2018). This step reparametrized each PSU into a set of community-weighted mean and proportional values for quantitative and qualitative traits, respectively. We then scaled each of the three quantitative trait means by their respective maximum value (e.g. trophic position_{*j*}/trophic position_{max}). This constrained all the community-weighted trait values in the [0–1] closed interval and prevented any single trait term from numerically dominating analyses. Each qualitative trait was converted to a binary dummy-matrix prior to CWM calculations (see *functcomp* and *dbFD* in Laliberté et al. 2014 for details).

Analytical methodology

To address our first question about whether there were composition-based differences between artificial and natural reef fish assemblages, we used a combination of univariate and multivariate analyses. First, we used linear mixed-effects models to evaluate the mean richness and fourth-root transformed density of reef fishes, independently. Each model included four factors: Type (fixed; 2 levels: artificial and natural), Depth (fixed; 2 levels: shallow and deep), Year (random; 10 levels: 2013–22), and Season (random; 4 levels: winter, spring, summer, and fall). Year and Season were included to

account for repeated measures at reefs through time. Next, we used multifactor mixed-effects permutational multivariate analysis of variance (PERMANOVA; Anderson 2017) using the PERMANOVA tool in the PERMANOVA + add-on (Anderson et al. 2008) for PRIMER v7 (Clarke and Gorley 2015) to compare the composition and abundance of assemblages. Each PERMANOVA model consisted of three factors: Type (fixed; 2 levels: artificial and natural), Year (random; 10 levels: 2013–22), and Season (random; 4 levels: winter, spring, summer, and fall). Additionally, we included Sample Date, expressed as a decimal value of sampling year (e.g. 2014.2), as a random linear covariate to address any long-term temporal trends in assemblage composition (Peake et al. 2022). We generated separate PERMANOVA models for shallow and deep reefs to account for depth-related assemblage differences that would have otherwise obscured interpretability of the fixed effect of Type (Menezes et al. 2006, Brokovich et al. 2008, Stefanoudis et al. 2019). We performed these PERMANOVAs using square-root transformed Bray-Curtis dissimilarities of the fourth-root transformed density data which included a dummy variable with a value = 1 (Clarke et al. 2006). Bray-Curtis dissimilarity was well-suited for handling composition and abundance data (Faith et al. 1987, Clarke et al. 2006). Furthermore, the square root-transformation coerced the semimetric Bray-Curtis dissimilarity into a metric form and therefore provided a more conservative estimate of variance explained by each PERMANOVA model (Legendre and Anderson 1999, Legendre and Legendre 2012). We checked for homogeneity of multivariate dispersion by Type using the PER-MDISP tool in the PERMANOVA + add-on for PRIMER v7.

We also generated canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) ordinations to visualize the multivariate structure of any PERMANOVA models that indicated a significant effect of Type. We used the Biodi*versityR* (Kindt and Coe 2005) and *ggplot2* (Wickham 2016) packages in R to generate these ordinations. Since a two-level grouping factor requires only one canonical axis to represent differences between levels, we included a jittered vertical axis to facilitate a two-dimensional visualization. We also included correlation biplot vectors in each CAP ordination to help illustrate the taxa that most effectively differentiated assemblages between the two reef types within each depth. To determine which taxon vectors to include in each CAP ordination, we performed indicator value analysis (Dufrene and Legendre 1997) using the *vegan* package (Oksanen et al. 2020). This index uses the derived values of specificity and fidelity to objectively identify those taxa that best characterize each level of a grouping factor using the following equation:

where $IndVal_{i,j}$ is the indicator value of taxon *i* for level *j* of a grouping factor, $A_{i,j}$ is the proportion of taxon *i* present in level *j* (specificity), and $B_{i,j}$ is the proportion of samples in level *j* that contain species *i* (fidelity). A permutational significance test is used to determine whether the maximum indicator value of *j* indicator values for taxon *i* would be observed by random chance. A perfect indicator taxon is one where all the individuals occur in a single level of a grouping factor and those individuals occur in all the samples within that level (Dufrene and Legendre 1997). We applied a sequential Bonferroni correction to all indicator value taxon tests of significance to account for multiple testing (Holm 1979).

To address our second question about whether there were trait-based differences between artificial and natural reef fish assemblages, we applied the same PERMDISP, PER-MANOVA, and CAP ordination methodologies described above to square-root transformed Bray–Curtis dissimilarities of the community-weighted trait data. Although these data were constrained in the [0–1] interval, they were directly derived from composition and abundance data and could have therefore contained artifacts (e.g. false zeros) which made Bray–Curtis dissimilarity an appropriate resemblance measure. We based all permutational tests of significance on 10 000 iterations and $\alpha = 0.05$.

Results

General results

Our survey efforts resulted in 151 and 148 PSUs for shallow and deep reefs, respectively. We observed a total of 162 distinct taxa among those 299 PSUs. However, we only retained 77 taxa after application of the 5% threshold within depths, comprising 70 taxa identified to species, 5 to genus, 1 to suborder, and 1 to family (Table S1). Forty-two of those 77 taxa (54.5%) were observed on both shallow and deep reefs, whereas 9 (11.7%) and 26 (33.8%) were exclusively observed at shallow and deep reefs, respectively (Table S1). There was a significant Type × Depth interaction for mean richness (t = 2.50, p < 0.05). However, this appeared to be primarily influenced by the greater mean richness per PSU exhibited by deep natural reefs $(23.73 \pm 0.56 \text{ taxa})$ relative to deep artificial reefs (20.85 \pm 0.78 taxa; post-hoc contrast: t = 3.81, p < 0.01), whereas shallow artificial and natural reefs had similar richness (15.46 \pm 0.47 and 15.71 \pm 0.45 taxa, respectively; post-hoc contrast: t = 0.30, p = 0.99; Fig. 2a). In contrast, the mean total density of reef fishes was greater on artificial reefs $(1.44 \pm 0.04 \text{ no./m}^2)$ than natural reefs (1.12 ± 0.03) no./m²; Type: t = 4.99, p < 0.01), a pattern that was consistent with depth (Type \times Depth interaction: t = 0.38, p = 0.70; Fig. 2b).

Composition and abundance

The shallow- and deep-reef composition and abundance data each met the assumption of homogeneity of multivariate dispersion for the fixed effect of Type (PERMDISP, all p > 0.13). The composition and abundance of fishes at shallow reefs varied by Type, Year, and Season (PERMANOVA, all p < 0.05; Table 3). Although there was a significant Type × Year interaction, the fixed effect of Type explained nearly three times more variability in the taxonomic diversity of reef assemblages (Table 3). The separation between artificial and natural reef assemblages was apparent in the



Figure 2. Descriptive univariate statistics (mean \pm 95% CI) by reef type and depth.

CAP ordination (Fig. 3a). Of the 51 distinct taxa observed on shallow reefs, indicator value analysis identified 16 significant taxa (31%) that best characterized differences between shallow artificial- and natural-reef fish assemblages (Table 4). Although many of those taxa had moderate-to-lower indicator values, it does not mean that they were poor indicators of reef type. For example, a closer inspection of the underlying specificity and fidelity values revealed that *Centropomus undecimalis* (common snook; $IndVal_{Art} = 0.31$) was exclusively observed on artificial reefs (specificity_{Art} = 1.00) even though it was absent in majority of the PSUs representing that reef type (fidelity_{Art} = 0.31). Thus, despite its relatively low indicator value, the presence of *C. undecimalis* was a reliable indicator that the PSU originated on a shallow artificial reef.

The composition and abundance of reef fishes at deep reefs also varied by Type and Year (PERMANOVA, all p < 0.05) but were consistent by Season (PERMANOVA, p > 0.05; Table 3). Like the shallow reefs, there was a significant Type × Year interaction (PERMANOVA, p < 0.05). However, this interaction explained an order of magnitude less variability than the fixed effect of Type. Specifically, the effect of Type accounted for nearly 25% of the variability in the taxonomic diversity of among deep-reef assemblages. Additionally, the significant Type × Season interaction term explained zero variability after correcting for components with negative variance estimates (Fletcher and Underwood 2002, Anderson 2017). The CAP ordination revealed very little overlap between deep artificial and natural reef assemblages (Fig. 3b). Of the 68 distinct taxa observed on deep reefs, indicator

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Table 3. Multifactor mixed-effects PERMANOVA results for composition and abundance data.

Source	Component	df	Sum of squared deviations	Mean square	Pseudo-F	<i>p</i> -value	Variance estimate	Percent of total
Shallow reefs								
Sample Date (covariate)	Random	1	114.32	114.32	2.88	0.0001	0.73	7.69
Туре	Fixed	1	227.30	227.30	6.07	0.0001	1.65	17.39
Year	Random	9	338.53	37.61	1.48	0.0001	0.98	10.30
Season	Random	3	159.65	53.22	2.64	0.0001	1.15	12.11
Type x Year	Random	9	197.09	21.90	1.27	0.0013	0.57	5.97
Type x Season	Random	3	53.26	17.75	1.04	0.3797	0.00	0.00
Type x Year x Season	Random	26	446.60	17.18	0.85	0.9998	0.00	0.00
Residual		98	1973.90	20.14			4.41	46.53
Total		150	3510.70				9.49	100.00
Deep reefs								
Sample Date (covariate)	Random	1	81.86	81.86	2.11	0.0024	0.56	5.95
Туре	Fixed	1	403.20	403.20	9.31	0.0001	2.27	24.23
Year	Random	9	321.67	35.74	1.45	0.0001	0.97	10.34
Season	Random	3	89.11	29.70	1.26	0.0546	0.55	5.90
Type x Year	Random	9	205.74	22.86	1.34	0.0002	0.30	3.25
Type x Season	Random	3	63.94	21.32	1.26	0.0261	0.00	0.00
Type x Year x Season	Random	25	425.13	17.01	0.72	1.0000	0.00	0.00
Residual		96	2260.80	23.55			4.71	50.32
Total		147	3851.50				9.36	100.00

Note: Results were based on square-root transformed Bray–Curtis dissimilarity of fourth-root transformed reef fish densities. Variance components were calculated after the sequential removal of terms with a negative variance estimate, setting their contributions to zero (Fletcher and Underwood 2002, Anderson 2017).

value analysis identified 29 significant taxa (43%) that best characterized differences between deep artificial and natural reefs (Table 5). Like the shallow reefs, many of those taxa had moderate-to-low indicator values. Of note was the substantial indicator value of 0.90 for *Haemulon aurolineatum* (tomtate) on deep artificial reefs. This suggested that the presence of *H. aurolineatum* was a very strong indication that the PSU originated on a deep artificial reef.

Trait-based functional diversity

The shallow- and deep-reef community-weighted trait data each met the assumption of homogeneity of multivariate dispersion for the fixed effect Type (PERMDISP, all p > 0.09). Trait-based functional diversity of shallow reefs differed by Type, with some additional variability attributed to Season and Year (PERMANOVA, all p < 0.05; Table 6). The fixed effect of Type explained the greatest amount of variability in functional diversity among shallow assemblages (Table 6). Shallow artificial reefs were generally characterized by greater densities of taxa with relatively greater length_{max} and caudal fin aspect ratio, as well as fusiform lateral profiles, oval crosssectional profiles, terminal mouths, and an affinity toward soft-bottom substrate. In contrast, shallow natural reefs were characterized by greater densities of taxa with deep or elongated lateral profiles, circular or compressed cross-sectional profiles, superior or subterminal mouths, and an affinity toward mixed- or hard-bottom substrate (Figs. 4a, 5). Last, although the correlation vector for trophic position was shifted toward natural reefs, its horizontal magnitude was substantially smaller than any other trait. It was therefore unlikely that the mean trophic position of assemblages differed substantially between shallow artificial and natural reefs.

The community-weighted trait data for deep-reef assemblages also differed by Type and Year (PERMANOVA, all p < 0.05; Table 6). Although the interaction of Type × Year was again significant, it also contributed zero variability to the functional diversity of assembalges after accounting for negatives variance estimates (Fletcher and Underwood 2002, Anderson 2017). Type accounted for nearly 28% of the variability in functional diversity among deep reefs, and that group separation was reflected well in the CAP ordination. Deep artificial reefs were generally characterized by greater densities of taxa with relatively greater length_{max}, trophic position, and caudal fin aspect ratio as well as fusiform lateral profiles, terminal mouths, and an affinity toward soft-bottom substrate. In constrast, deep natural reefs were characterized by taxa with deep or elongated lateral profiles, circular cross-sectional profiles, superior or subterminal mouths, and an affinity toward mixed-bottom substrate (Figs. 4b, 6). Taxa with angular, oval, compressed, and flattened cross-sectional profiles or an affinity toward hard-bottom substrate were likely less influential on differences between deep artificial and natural reefs. Additionally, the lateral profile and mouth position classifications "other" and "inferior" were solely attributed to the infrequently observed Hypanus americanus (southern stingray). Therefore, these two classifications contributed little to overall differences in functional diversity between deep artificial and natural reefs.

Discussion

In this study, we conducted a comprehensive investigation of reef fish assembly patterns on artificial and natural reefs using a long-term visual survey dataset. Our analyses revealed significant variability in the taxonomic and functional diversity of these assemblages between reef types. Specifically, our findings demonstrated that artificial reefs consistently hosted greater reef fish densities, regardless of species identity. Additionally, our results highlighted a distinct pattern where



Figure 3. CAP ordinations for reef fish composition and abundance. Percentages shown next to each subtitle indicate the total percentage of variability in the taxonomic diversity of shallow (a) and deep (b) reef assemblages captured by the respective CAP model. The horizontal magnitude of each vector is proportional to its correlation with CA1, and the numbers correspond to the IDs provided in Tables 4 (shallow) and 5 (deep).

fable 4. Significant indicator value taxa and their com	onent specificity and fidelity values for shallow reefs by reef type.
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ID	Scientific name	Common name	Reef type	IndVal	Specificity	Fidelity	<i>p</i> -value
71	Diplodus holbrookii	spottail pinfish	Artificial	0.66	0.73	0.91	0.0051
8	Decapterus spp.	scad species	Artificial	0.51	0.81	0.63	0.0051
24	Haemulon aurolineatum	tomtate	Artificial	0.49	0.78	0.63	0.0051
18	Chaetodipterus faber	Atlantic spadefish	Artificial	0.42	0.95	0.44	0.0051
13	Centropomus undecimalis	common snook	Artificial	0.31	1.00	0.31	0.0051
76	Sphoeroides spengleri	bandtail pufferfish	Artificial	0.27	0.78	0.35	0.0120
60	Epinephelus itajara	goliath grouper	Artificial	0.21	0.89	0.24	0.0051
73	Sphyraena barracuda	great barracuda	Artificial	0.20	0.95	0.21	0.0051
23	Anisotremus virginicus	porkfish	Artificial	0.13	1.00	0.13	0.0296
74	Sphyraena guachancho	guaguanche barracuda	Artificial	0.12	1.00	0.12	0.0266
61	Epinephelus morio	red grouper	Natural	0.55	0.75	0.72	0.0051
49	Stegastes variabilis	cocoa damselfish	Natural	0.48	0.65	0.74	0.0051
75	Synodus intermedius	sand diver	Natural	0.44	0.72	0.62	0.0051
53	Pareques umbrosus	cubbyu	Natural	0.42	0.70	0.61	0.0120
3	Balistes capriscus	gray triggerfish	Natural	0.38	0.91	0.42	0.0051
20	Coryphopterus glaucofraenum	bridled goby	Natural	0.26	0.75	0.34	0.0396

Note: ID corresponds to the same value provided in Table S1.

Table 5. Significant indicator value taxa and their component specificity and fidelity values for deep by reef type.

ID	Scientific name	Common name	Reef type	IndVal	Specificity	Fidelity	<i>p</i> -value
24	Haemulon aurolineatum	tomtate	Artificial	0.90	0.92	0.97	0.0068
73	Sphyraena barracuda	great barracuda	Artificial	0.68	0.97	0.70	0.0068
60	Epinephelus itajara	goliath grouper	Artificial	0.57	0.75	0.76	0.0068
11	Seriola dumerili	greater amberjack	Artificial	0.54	0.67	0.81	0.0068
12	Seriola rivoliana	almaco jack	Artificial	0.47	0.70	0.68	0.0068
34	Rhomboplites aurorubens	vermilion snapper	Artificial	0.43	0.91	0.47	0.0068
33	Ocyurus chrysurus	yellowtail snapper	Artificial	0.41	0.79	0.51	0.0068
6	Caranx crysos	blue runner	Artificial	0.33	0.76	0.43	0.0094
18	Chaetodipterus faber	Atlantic spadefish	Artificial	0.30	0.86	0.35	0.0068
23	Anisotremus virginicus	porkfish	Artificial	0.27	0.96	0.28	0.0068
32	Lutjanus synagris	lane snapper	Artificial	0.15	1.00	0.15	0.0336
27	Halichoeres bivittatus	slippery dick	Natural	0.62	0.68	0.92	0.0068
25	Haemulon plumierii	white grunt	Natural	0.57	0.61	0.93	0.0068
67	Serranus subligarius	belted sandfish	Natural	0.56	0.69	0.81	0.0068
14	Chaetodon ocellatus	spotfin butterflyfish	Natural	0.52	0.68	0.76	0.0068
57	Cephalopholis cruentata	graysby	Natural	0.52	0.61	0.85	0.0308
61	Epinephelus morio	red grouper	Natural	0.51	0.81	0.64	0.0068
49	Stegastes variabilis	cocoa damselfish	Natural	0.51	0.63	0.81	0.0068
3	Balistes capriscus	gray triggerfish	Natural	0.50	0.97	0.51	0.0068
62	Hypoplectrus spp.	hamlet species	Natural	0.43	0.73	0.59	0.0068
20	Coryphopterus glaucofraenum	bridled goby	Natural	0.41	0.72	0.57	0.0068
30	Lutjanus campechanus	red snapper	Natural	0.38	0.85	0.45	0.0068
44	Chromis scotti	purple reeffish	Natural	0.37	0.86	0.43	0.0068
70	Calamus spp.	porgy species	Natural	0.36	0.71	0.51	0.0138
47	Stegastes partitus	bicolor damselfish	Natural	0.34	0.84	0.41	0.0068
26	Haemulon spp.	grunt species	Natural	0.28	0.75	0.38	0.0308
39	Opistognathus aurifrons	yellowhead jawfish	Natural	0.26	0.77	0.34	0.0492
58	Diplectrum formosum	sand perch	Natural	0.18	0.90	0.20	0.0225

Note: ID corresponds to the same value provided in Table S1.

Table 6. Multifactor mixed-effects PERMANOVA results for trait-based functional diversity.

Source	Component	df	Sum of squared deviations	Mean square	Pseudo-F	<i>p</i> -value	Variance estimate	Percent of total
Shallow reefs								
Sample date (covariate)	Random	1	12.17	12.17	2.30	0.0009	0.22	6.06
Туре	Fixed	1	41.96	41.96	5.86	0.0001	0.71	19.28
Year	Random	9	45.11	5.01	1.21	0.0292	0.27	7.23
Season	Random	3	19.44	6.48	1.75	0.0005	0.33	9.11
Type x Year	Random	9	33.58	3.73	1.13	0.1442	0.13	3.42
Type x Season	Random	3	11.62	3.87	1.17	0.1794	0.12	3.23
Type x Year x Season	Random	26	85.86	3.30	0.89	0.9684	0.00	0.00
Residual		98	361.85	3.69			1.90	51.67
Total		150	611.59				3.68	100.00
Deep reefs								
Sample date (covariate)	Random	1	12.25	12.25	1.87	0.0269	0.20	5.69
Туре	Fixed	1	76.95	76.95	10.36	0.0001	0.99	27.89
Year	Random	9	53.41	5.93	1.48	0.0026	0.39	11.07
Season	Random	3	10.43	3.48	0.84	0.7557	0.00	0.00
Type x Year	Random	9	34.90	3.88	1.27	0.0081	0.00	0.00
Type x Season	Random	3	11.04	3.68	1.21	0.1104	0.00	0.00
Type x Year x Season	Random	25	76.11	3.04	0.74	1.0000	0.00	0.00
Residual		96	396.13	4.13			1.97	55.34
Total		147	671.21				3.56	100.00

Note: Results were based on square-root transformed Bray–Curtis dissimilarity of community-weighted trait values which were calculated using fourthroot transformed density data. Variance components were calculated after the sequential removal of terms with a negative variance estimate, setting their contributions to zero (Fletcher and Underwood 2002, Anderson 2017).



Figure 4. CAP ordinations for trait-based functional diversity. Percentages shown next to each subtitle indicate the total percentage of variability in the functional diversity of shallow (a) and deep (b) reef assemblages captured by the respective CAP model. The horizontal magnitude of each vector is proportional to its correlation with CA1. Trait abbreviations: MP, mouth position; LP, lateral profile; CS, cross-sectional profile; and ST, preferred substrate.

Artificial		Natural
	Length _{max}	
	Trophic position	
	Caudal fin aspect ratio	•
Fusiform	Lateral profile	Deep/Elongated
Oval	Cross-sectional profile	Circular/Compressed
Terminal	Mouth position	Superior/Subterminal
Soft	Preferred substrate	Mixed/Hard
**	Representative examples	+

Figure 5. Summary of community-weighted trait patterns for shallow artificial and natural reefs. Note that the representative examples are not drawn to scale, and that they represent a small subset of potential morphological forms that broadly reflect the traits which characterize the respective reef type.

Artificial		Natural
	Length _{max}	
	Trophic position	
	Caudal fin aspect ratio	
Fusiform	Lateral profile	Deep/Elongated
-	Cross-sectional profile	Circular
Terminal	Mouth position	Superior/Subterminal
Soft	Preferred substrate	Mixed
	Representative examples	H

Figure 6. Summary of community-weighted trait patterns for deep artificial and natural reefs. Note that the representative examples are not drawn to scale, and that they represent a small subset of potential morphological forms that broadly reflect the traits which characterize the respective reef type.

functional traits typically indicative of midwater or transient predatory taxa were more prevalent on artificial reefs, whereas characteristic features of mesopredators and smaller-bodied reef dwellers were more frequently observed on natural reefs. In this discussion, we provide a deeper context for these results and how they may offer insight into future applications of artificial reefs in the eastern Gulf of Mexico as well as other subtropical systems globally.

The observed difference in mean fish density between reef types may be related to the structural characteristics of the study reefs. Although we did not explicitly measure the spatial area of our reefs, many of the natural reefs in the eastern Gulf of Mexico are relic shorelines that can be several meters wide and span distances of hundreds of meters (Hine et al. 2008, Hine and Locker 2011). In contrast, artificial reefs tend to have relatively smaller footprints (Patterson et al. 2014), often determined by the materials used or permitted deployment locations. Consequently, reef fishes are likely to exploit resources over a much larger area on natural reefs, whereas they may be concentrated within the relatively limited spatial extent of structured habitat on artificial reefs (Patterson et al. 2014, Karnauskas et al. 2017, Garner et al. 2019). The observed disparity in fish densities by reef type has important implications for the perceived catchability and management of various taxa (Patterson et al. 2014, Karnauskas et al. 2017). Specifically, it remains unclear whether these artificial reefs may enhance the standing biomass of popular sport fishes or contribute to potential overfishing by concentrating biomass in relatively small areas (e.g. Grossman et al. 1997, Lindberg 1997, Cowan et al. 2011, Patterson et al. 2014, Karnauskas et al. 2017, Layman and Allgeier 2020).

In addition to the observed difference in mean reef fish density, our results revealed that the artificial and natural reefs in the present study supported compositionally and functionally distinct assemblages. Artificial reefs supported relatively greater densities of larger-bodied fishes with higher caudal fin aspect ratios, fusiform bodies, and terminal mouths. In contrast, natural reefs were characterized by smaller-bodied fishes with lower caudal fin aspect ratios, less streamlined bodies, and either superior or subterminal mouths. These differences reflect adaptive responses of fishes to their environments. For example, fishes that rely upon infrequent, yet densely populated patches of prey have evolved morphological traits which help to minimize the energy expended in searching for and chasing down prey, such as streamlined bodies and higher caudal fin aspect ratios. Conversely, fishes in environments with locally abundant prey exhibit traits that maximize maneuverability (i.e. low caudal fin aspect ratio) or facilitate specialized feeding (Webb 1984, 1988). Additionally, there is a positive relationship between caudal fin aspect ratio and food consumption in marine fishes (Pauly 1989a, 1989b), and largerbodied taxa often have elevated trophic positions (Hayden et al. 2019). Although our selection of traits may have constrained the observable outcomes due to these associations, we concluded that artificial reefs supported relatively greater densities of transient or midwater predators, whereas demersal mesopredators or invertivores were relatively more abundant on natural reefs.

The reported differences between artificial and natural reef assemblages highlight the dynamic processes that influence assembly patterns and led us to infer that physical habitat characteristics may have played a substantial role in structuring these assemblages (i.e. local-scale habitat filtering). Indeed, previous studies have evaluated the influence of vertical relief and structural complexity on reef fish diversity (Simon et al. 2013, Patterson et al. 2014, Garner et al. 2019, Paxton et al. 2020b), and Wall and Stallings (2018) previously reported that the artificial reefs in this study exhibited greater vertical relief than their natural counterparts. Specifically, the vertical relief of shallow artificial reefs was 2–3 times greater than nearby natural reefs, and deep artificial reefs had nearly an order of magnitude greater relief relative to deep natural reefs (Wall and Stallings 2018). Consequently, the greater vertical relief on artificial reefs provides a more three-dimensional habitat which may be beneficial to taxa with three-dimensional foraging patterns and low site fidelity, such as transient or midwater predators (Paxton et al. 2020b).

It is also worth considering the uniformity of materials used in the development of artificial reefs and whether those materials adequately replicate the physical characteristics of natural habitats (e.g. Carr and Hixon 1997, Granneman and Steele 2015, Paxton et al. 2020a). The deep artificial reefs in our study primarily consisted of large, repurposed steel-hulled vessels. Although such vessels contain large internal cavities, they tend to lack the small spaces that are commonly found on natural reefs (Patterson et al. 2014). Therefore, small-bodied reef fishes, such as damselfishes, blennies, or the juvenile stages of more conspicuous taxa (e.g. snapper, grunts, and groupers), may be exposed to increased predation risk on artificial reefs (Patterson et al. 2014). This may lead to a shift in predatorprey dynamics which favors increased predator abundances as the availability of prey refugia decreases (Grabowski 2004). The relatively greater mean trophic position of deep artificialreef assemblages supports this conclusion, and agrees with elevated predator densities on artificial reefs observed by Paxton et al. (2020b). However, assemblage mean trophic position was relatively similar among the shallow reefs in this study. A potential explanation may be the materials used to develop those artificial reefs. Despite the use of materials which naturally lack interstitial spaces (i.e. non-porous concrete rubble), the systematic placement of those materials during artificial reef deployment may have resulted in some of the medium-tosmall refugia suitable for smaller bodied reef fishes to forage or avoid predation.

In addition to the roles of habitat and predator-prey dynamics, fishing may have contributed to the observed differences in reef fish assemblages between reef types (e.g. Blanchard et al. 2005, Russ et al. 2005, Wilson et al. 2008, 2010). Simard et al. (2016) previously quantified boater visitation rates on our eight study reefs and revealed that the artificial reefs received more frequent visits compared to the natural reefs. Specifically, artificial reefs were visited roughly 2-10 times more frequently than nearby natural reefs (Simard et al. 2016). It was presumed that boaters primarily visited these reefs for recreational fishing, and the differences in visitation rates were therefore likely influenced by two factors. First, artificial reefs are often easily accessible to boaters because their coordinates are publicly available online. Second, perceived catch rates of targeted species tend to be higher at artificial reefs (Karnauskas et al. 2017), a circumstance that is likely associated with the previously discussed differences in fish densities by reef type. When considered together, these findings agree with prior work which suggest that fishing effects may be modulated by abiotic habitat features in structuring reef fish assemblages (Wilson et al. 2008, 2010).

There are a variety of other factors to consider when comparing reef assemblage patterns on artificial and natural reefs. For example, Wall and Stallings (2018) demonstrated the role of urchin grazing in structuring the epibenthic communities of our eight study reefs. The quantity and types of primary production on these reefs may further influence predator-prey dynamics (e.g. Horinouchi et al. 2009, Jaxion-Harm and Speight 2012). Additionally, our data comprise a decade of visual survey data collected at regular intervals, and we are aware of the well-documented effects of stochastic or persistent perturbations on assemblage patterns (Levin and Paine 1974, Connell et al. 1997, Wilson et al. 2006, Commander and White 2019). Although we included time as both continuous and categorical predictors in our PERMANOVA models, it remains unclear whether any particularly notable events had significant or long-lasting effects or whether those effects were consistent across reef type. For example, two severe harmful algal blooms occurred in the eastern Gulf of Mexico during the study period, and several major hurricanes (i.e. category 3 or greater) passed through the region as well. Moreover, Midway et al. (2021) reported that recreational angling increased throughout the USA during the earliest portion of the COVID-19 pandemic, and prior evidence already suggests that artificial reefs are visited more often than natural reefs (Simard et al. 2016). Last, there is a growing body of literature that discusses how the geographic distributions of taxa have shifted in response to global climate change (Fodrie et al. 2010, Bates et al. 2013, Purtlebaugh et al. 2020). Each of these factors warrant further investigation since they may have complex and varying effects on reef fish assemblages in this region.

The results of our study suggested that artificial reefs in the eastern Gulf of Mexico may be fundamentally different than natural reefs. However, we must consider the primary objective(s) that guide the development and placement of artificial reefs when making such conclusions (Lima et al. 2019, Paxton et al. 2020a). Many of Florida's artificial reefs are strategically placed to support ecotourism or enhance commercial and recreational fisheries, all while simultaneously supporting the long-term sustainability of fisheries species (FWC Division of Marine Fisheries 2003). Previous research on our study reefs has demonstrated their success at supporting ecotourism (Simard et al. 2016), and their apparent resilience to largescale physical perturbations (e.g. major hurricanes) suggests that they may contribute to the long-term health of local marine assemblages. In the present study, artificial reefs appeared to support relatively greater densities of some popular sport fishes such as Lutjanus griseus (gray snapper), C. undecimalis (common snook), and Seriola dumerili (greater amberjack). Such artificial reefs may therefore be deemed "successful" with respect to supporting ecotourism or enhancing fisheries. However, natural reefs appeared to support relatively greater densities of other valuable sport fishes, such as Epinephelus morio (red grouper) and L. campechanus (red snapper), which are two of the most highly targeted species in the region (Stallings et al. 2023b). It may be that the artificial reefs in the present study lacked features sufficient to support greater densities of those taxa and could therefore be considered "unsuccessful." In either case, these findings tend to agree with Paxton et al. (2020a) that artificial reefs are "not a one-size-fits-all tool." Additionally, it is still unclear whether these artificial reefs enhance secondary production, thereby benefiting the overall health of fisheries species, or concentrate individuals, thereby contributing to potential overfishing (i.e. "production vs. attraction"; Lindberg 1997). Indeed, many harvested fishes are either overfished or subject to overfishing, which would imply that their populations may be limited by recruitment rather than habitat availability (Grossman et al. 1997). The complex interplay between artificial reefs and fisheries dynamics, habitat restoration, and biodiversity preservation underscores the need for a nuanced and multifaceted approach to reef management and conservation.

Conclusions

The visual survey data presented in this study are among the longest of which we are aware for paired artificial and natural reefs and were collected with consistent methods at regular intervals. Our approach, which concurrently analyzed composition- and trait-based diversity, expanded our ability to infer processes that may structure the fish assemblages supported by these reefs. Although we acknowledge the importance of intraspecific trait variability, such measurements are often impractical with the survey methods that we used. For instance, accurate estimates of trophic position often require gut content or tissue stable isotope analyses (e.g. Stallings et al. 2023a). We therefore concluded that proxy estimates were suitable for this comparative study, and we encourage other researchers to consider similar approaches within their respective focal systems. Our findings revealed distinct differences in the composition and abundance of artificial and natural reef fish assemblages, and these differences were reflected in the dominant functional forms that characterized those assemblages. This led us to infer the likelihood of a few factors as the primary contributors to assemblage variability between artificial and natural reefs: differences in structural complexity and vertical relief, shifts in predator-prey dynamics that result from those differences in structural complexity, and asymmetric fishing intensity. Unlike composition and abundance data, functional diversity estimates are less sensitive to regionally distinct taxa pools and therefore allows for more broadly generalized results applicable to other systems (e.g. other subtropical reefs around the world). However, we also acknowledge that a larger study area with additional reefs would have strengthened our results. Nonetheless, artificial reefs, as well as other human-made structures, continue to be used to meet a variety of stakeholder and management objectives. This trend has gained momentum in recent decades and shows no signs of decline in the near future. It is therefore important that we continue to monitor and evaluate the role of human-made structures with respect to stakeholder interests, management objectives, and the overall biodiversity of the ecosystems that we so heavily rely upon.

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Author contributions

Michael J. Schram: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing original draft, writing - review & editing. Meaghan E. Emory: investigation, writing - review & editing. Joshua P. Kilborn: formal analysis, writing - review & editing. Jonathan A. Peake: formal analysis, investigation, writing - review & editing. Kara R. Wall: investigation, data curation, writing - review & editing. Ian Williams: investigation, writing - review & editing. Christopher D. Stallings: conceptualization, Funding acquisition, investigation, project administration, supervision, writing - review & editing.

Supplementary material

Supplementary data is available at ICES Journal of Marine Science online.

Conflict of interest

The authors have no conflicts of interest to declare.

Data availability

Analytical code and data: https://github.com/MichaelJSchra m/ArtNatReef_Code.

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