Trophic ecology of red snapper *Lutjanus campechanus* on natural and artificial reefs: interactions between annual variability, habitat, and ontogeny

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ABSTRACT: In the Gulf of Mexico (GOM), oil and gas platforms have created an expansive network of artificial reefs. Generally, policies mandate removal of these structures post-production; however, many enter 'Rigs-to-Reefs' (RTR) programs that convert the rig materials into artificial reefs ('reefing'). Despite the growth of RTR programs worldwide, the functionality of the resulting habitats remains uncertain, particularly due to the lack of comparative studies with natural systems. To address this data gap as it relates to trophic ecology, we compared annual, ontogenetic, and habitat-specific diet and stable isotope signatures (δ^{13}C and δ^{15}N) of adult red snapper *Lutjanus campechanus* (n = 1585) from relic coralgal natural reefs to those of fish from standing and reefed platforms located in similar depth strata of the northwestern GOM. Stomach content analyses revealed significant effects of year, habitat, and total length on prey composition. Subsequent analyses of stable isotope values by size class identified a non-linear relationship with ontogeny. δ^{13}C and δ^{15}N values at reefed platforms and natural reefs decreased in the medium size class (401–600 mm total length), whereas fish from standing platforms exhibited more consistent feeding patterns across ontogeny. Annual variability was also observed in δ^{13}C and δ^{15}N values, with 2013 and 2014 significantly different from 2015. These findings suggest that the trophic impacts of habitat type on reef fishes are more complex than previously considered in the GOM and that reefed platforms provide foraging opportunities more similar to natural reefs than standing platforms.

KEY WORDS: Trophic level · Niche width · Stomach content · Stable isotopes · Diet

1. INTRODUCTION

Habitat complexity is important to reef fish for a number of reasons, including provision of shelter from predation and food resources. Thus, a lack of complex benthic habitat (i.e. coral reefs, banks, etc.) is often considered to be a limiting factor for many reef fish populations. This is especially apparent in the northwestern Gulf of Mexico (GOM), which is composed primarily of soft-bottom habitat with few distinct areas of high-relief natural reef (Parker et al. 1983). In this region of the GOM, artificial structures,

such as oil and gas platforms, represent the dominant complex habitat (Ajemian et al. 2015). As such, these high-relief, artificial habitats are surrounded by rich communities of marine life (Scarborough Bull & Kendall 1994, Jørgenson 2009, Ajemian et al. 2015, Streich et al. 2017a), which has also been demonstrated in other locations, such as the North Sea (Guerin et al. 2007, Fujii 2016), southern California (Claisse et al. 2014, Bull & Love 2019), and northwest Australia (Pradella et al. 2014).

When platforms cease to be used for oil and gas production, companies are responsible for decom-

missioning the structure, which may entail complete removal, relocation, and/or conversion of the platform into an artificial reef ('reefing'). Some decommissioned platforms enter artificial reef programs, such as 'Rigs-to-Reefs' (RTR), where a portion of the structure is retained in the ocean with the intent of preserving the created habitat for fisheries enhancement and other uses, like the creation of SCUBA diving opportunities. For these conversions, the 'jacket' of the rig is modified from spanning the entire water column (ocean floor to above the water surface) into a lower-relief configuration by either toppling the structure or removing the upper portion (Scarborough Bull & Kendall 1994, Kaiser & Pulsipher 2005).

The highest offshore oil and gas platform densities in the world are in the GOM, where ~40 000 platforms have been installed since the 1940s (Francois 1993). Official estimates for the GOM are 1903 operational oil and gas structures in place with ~4000 more decommissioned platforms (BSEE 2019). However, recent remote-sensing work has put the total count of platform installations higher at ~9260 (Liu et al. 2016). Due to the high density of aging oil and gas infrastructure in the GOM, approaches to decommissioning in this ocean basin have the potential to set global precedents. Currently, in the GOM, 515 platforms have been converted to permanent artificial reefs (BSEE 2019).

Though it is not possible to create additional natural hard bottom habitat, if reefed platforms provide similarly functioning habitat, then the conversion of standing platforms into artificial reefs may offer ecological benefits to fish populations. For example, in the North Sea, offshore platforms provide unique feeding opportunities that allow for interspecific prey resource partitioning that supports the diet of multiple species of fishes (Fujii 2016). Similarly, offshore of southern California, USA, platforms support populations of multiple rockfish species through provision of settlement grounds and a diverse prey base (Helvey 2002). Therefore, understanding the function of these platforms, both standing and reefed, in relation to fish populations and other marine life is essential because 'Idle Iron' policies have many platforms slated for removal (BSEE 2019). As the quality of habitat provided by these structures has not been well studied, there is a need for more information on how marine life use reefed platforms.

On standing and reefed platforms in the GOM, red snapper *Lutjanus campechanus* is often the dominant reef fish species (Stanley & Wilson 2003, Ajemian et al. 2015, Streich et al. 2017a); thus, it is a good indicator species for gauging the functionality of the

habitat. As with other reef-associated fishes, a lack of structured habitat is often considered to be a limiting factor to red snapper populations in the GOM (Shipp & Bortone 2009). Further, how red snapper use reefed platforms may be informative as to how other important, reef-associated species relate to platforms, including gray triggerfish *Balistes capriscus*, gray snapper *Lutjanus griseus*, vermilion snapper *Rhomboplites aurorubens*, greater amberjack *Seriola dumerili*, and scamp *Mycteroperca phenax*.

Despite the economic importance of the species, the trophic ecology of adult red snapper in the northwestern GOM (i.e. offshore of Texas) has not been well studied. The most comprehensive diet study in this region was conducted in the 1970s. In this study, 1139 red snapper were collected from undefined 'reef' sites with the majority of the samples coming from offshore of Port Aransas in depths of 40 to 100 m (see Fig. 1 here and Fig. 2 in Bradley & Bryan 1975). Fish were the most common prey reported in the diet of adults, followed by crustaceans, like the lesser blue crab *Callinectus danae* (Bradley & Bryan 1975). Much more recently, Dance et al. (2018) examined the trophic ecology of juvenile to small adult red snapper (145–570 mm total length [TL]) at nearshore (<60 km), relatively shallow (13–32 m) artificial reefs in the northwestern GOM near Galveston, TX. At these reefs, red snapper diet was primarily composed of stomatopods, fish, and portunid crabs (Dance et al. 2018). The main conclusions of both studies were that red snapper were generalist predators with diet reflective of prey availability.

More is known regarding red snapper trophic ecology in the north-central GOM, offshore of Louisiana and Alabama. In this region, red snapper are also considered to be generalist, opportunistic predators (Tarnecki & Patterson 2015, Foss 2016, Szedlmayer & Brewton 2019) known to consume a wide range of benthic organisms (McCawley & Cowan 2007, Wells et al. 2008, Schwartzkopf et al. 2017), as well as reef-associated prey (Ouzts & Szedlmayer 2003, Szedlmayer & Lee 2004, Schwartzkopf et al. 2017, Szedlmayer & Brewton 2019). At natural salt dome reefs, standing oil and gas platforms, and reefed platforms offshore of Louisiana, fish dominated the diet of red snapper, with those collected from natural reefs consuming the most diverse diet (Simonsen et al. 2015, Schwartzkopf et al. 2017). These sites varied substantially in underlying substrate (salt dome or delta mud) and complexity (Schwartzkopf et al. 2017), which may have affected the results as community assemblages on artificial reefs are known to change with these factors (Gallaway et al. 1981, Ajemian et al.

2015). Thus, the impact of habitat on red snapper diet remains unclear when other factors are similar.

Inconsistent ontogenetic shifts in red snapper diets have been observed throughout the GOM. For example, in some circumstances, juvenile red snapper (~ <60 mm TL) feed primarily on invertebrates (Bradley & Bryan 1975, Szedlmayer & Lee 2004, Wells et al. 2008); however, other studies have reported fish as the primary diet component (Tarnecki & Patterson 2015, Dance et al. 2018). On nearshore artificial reefs in the northwestern GOM, the percentage by weight (%W) of fish in the diet of red snapper decreases from juvenile fish to young adults, while the percentage of crustaceans increases (Dance et al. 2018). At other reef sites in the northwestern GOM, the opposite trend has been observed; juvenile red snapper primarily consume shrimp and other crustaceans, while the diet of adults is mostly fish (Bradley & Bryan 1975). Therefore, while ontogenetic changes in red snapper diet appear consistent, the exact differences in prey driving these shifts appear to be spatially and temporally variable.

An aspect that confounds red snapper diet research is that these fish are physoclistic and often suffer severe barotrauma from overexpansion of the swim bladder when brought to the surface from depth during collection (Bradley & Bryan 1975, Campbell et al. 2010, Curtis et al. 2015). This overexpansion results in eversion of the stomach and associated prey contents, which can create large gaps in the ability to comprehensively describe red snapper diet. For example, out of 1139 red snapper collected, 687 had everted stomachs, 262 stomachs were empty, and only 190 stomachs contained prey (Bradley & Bryan 1975). In an effort to account for data gaps created by loss of prey due to stomach eversion or challenges with identification, stable isotopes can provide information on temporally and spatially integrated trophic ecology (Layman et al. 2012). For example, stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in fish tissues vary in relation to consumed prey and have been used to understand energy flow on a longer time scale than gut content analysis (Fry 2006). $\delta^{13}C$ varies little per trophic level (<1‰), making it a good indicator of basal carbon sources, while $\delta^{15}N$ varies ~3.4‰ per trophic level, making it a good proxy for the relative trophic position at which an animal is feeding (Peterson & Fry 1987, Post 2002). Therefore, variations in $\delta^{15}N$ can be used to better understand red snapper trophic ecology and have been used in numerous studies in the GOM (Wells et al. 2008, Zapp Sluis et al. 2013, Simonsen et al. 2015, Tarnecki & Patterson 2015, Schwartzkopf et al. 2017, Dance et al. 2018).

Previous studies in the north-central GOM, offshore of Louisiana, have found red snapper from standing platforms often have elevated $\delta^{15}N$ compared to those from natural reefs and reefed platforms, possibly indicating red snapper at these habitats are feeding at higher trophic levels (Zapp Sluis et al. 2013, Simonsen et al. 2015, Foss 2016, Schwartzkopf et al. 2017). Despite this slight enrichment for standing platforms, the trophic niche of red snapper based upon the relationship of stable carbon and nitrogen isotopes suggest that a similar prey base exists among habitats in some geographic areas (Simonsen et al. 2015, Foss 2016). At natural and artificial reefs offshore of Alabama and Florida, there was no difference in stable isotope signatures in red snapper from natural and artificial reefs, although a trend of decreasing $\delta^{15}N$ with increasing size was observed (Tarnecki & Patterson 2015). Other studies of red snapper trophic ecology have recorded an opposite trend, wherein $\delta^{15}N$ increases with fish size (Wells et al. 2008, Zapp Sluis et al. 2013, Foss 2016).

Recent studies in the northwestern Gulf of Mexico have shown that reefed platforms support larger size-at-age red snapper relative to these natural reefs or standing platforms and that older, larger fish are found on the natural reefs (Streich et al. 2017b). Interestingly, for this same collection of fish, no significant differences in relative weight or reproductive biology were found among these 3 habitats (Downey et al. 2018). Thus, while these faster growth rates on reefed platforms do not also translate to significantly improved reproductive capacity or condition, it is possible that they are explained by higher-quality prey resources on these habitats. Therefore, in this study, we sought to better understand the feeding ecology of this same group of red snapper by evaluating the potential trophic enhancement provided by reefed platforms in the northwestern GOM over multiple years. This information will facilitate an understanding of how reefed platforms function ecologically, relative to a natural habitat, and the dynamics of these interactions over time. Further, this work also examined the diet of red snapper at a unique type of natural reef (relic coralgal vs. salt dome) that has not been previously studied.

2. MATERIALS AND METHODS

2.1. Study area

Red snapper were collected from 9 sites in the northwestern GOM, offshore of Texas. These sites

were selected to represent 3 habitat types (natural reefs, reefed platforms, and standing oil and gas platforms) in similar depth strata (60–90 m). In this region of the northwestern GOM, most natural reefs consist of drowned coralgal reefs with large expanses of hard substrate interspersed with sandy sediments and diverse invertebrate populations, including whip corals and sea fans (Rezak et al. 1985). Natural reef sites included Aransas Bank, South Baker Bank, and Baker Bank. Reefed and standing oil and gas platform sites were located in areas with mud bottom and little to no natural hard features. Reefed sites included MU-A-85, BA-A-132, and MI-A-7, while standing platform sites included MU-A-111, MU-A-85A, and BA-A-133 (Fig. 1).

2.2. Sample collection

Fishing was conducted following Southeast Area Monitoring and Assessment Program (SEAMAP) vertical-line protocols (SEAMAP 2013) in 3 randomly selected locations at each site per sampling day. Briefly, in each location, 9 vertical-line drops were conducted using 3 sets of long-line gangions, each equipped with varied hook sizes (8/0, 11/0, and 15/0) and baited with chunked Atlantic mackerel *Scomber*

scombrus (for more details, see Streich et al. 2017b). Each site was visited multiple times between May and September over 3 summer sampling seasons (2013, 2014, and 2015). Offshore sampling was not conducted regularly during other months of the year due to weather constraints. After capture, fish were stored on ice until processing (<24 h). In the lab, fish were weighed (nearest 0.01 kg), measured (mm), sexed, and dissected to collect biological samples, including otoliths, gonads, stomachs, and epaxial muscle tissue. Stomachs were initially placed whole into 10% formalin for at least 1 mo of preservation, after which the contents were removed and transferred to 70% ethanol.

2.3. Stomach content analysis

Following fixation, stomach contents were enumerated and identified to the lowest possible taxon (LPT), and individual prey items were weighed to the nearest 0.01 g. Otoliths, spines, and other hard structures were considered when present to help identify heavily degraded prey items. A vacuity index was calculated for all fish by comparing the number of red snapper containing prey to the total number collected. To serve as another measure of longer-term dietary information, gastric parasites encountered within the stomach were identified to LPT and enumerated (Locke et al. 2013). A percent by number (%N) of parasites was calculated by year, red snapper size class, and habitat. Unidentified content and non-prey items, such as plastic, were not considered in diet analyses. Percent frequency of occurrence (%FO), %N, and percent composition by weight (%W) were calculated for each identifiable prey type. Using these parameters, the index of relative importance (IRI = [%N + %W] × FO; Liao et al. 2001) and percent IRI (%IRI) were calculated. Cumulative prey curves were created in PRIMER-6 to assess sample size sufficiency by habitat. To identify if prey curves reached an asymptote, a linear regression was conducted on the last 4 points, and a slope (b) < 0.05 was considered to be representative of the diet (Bizzarro et al. 2007).

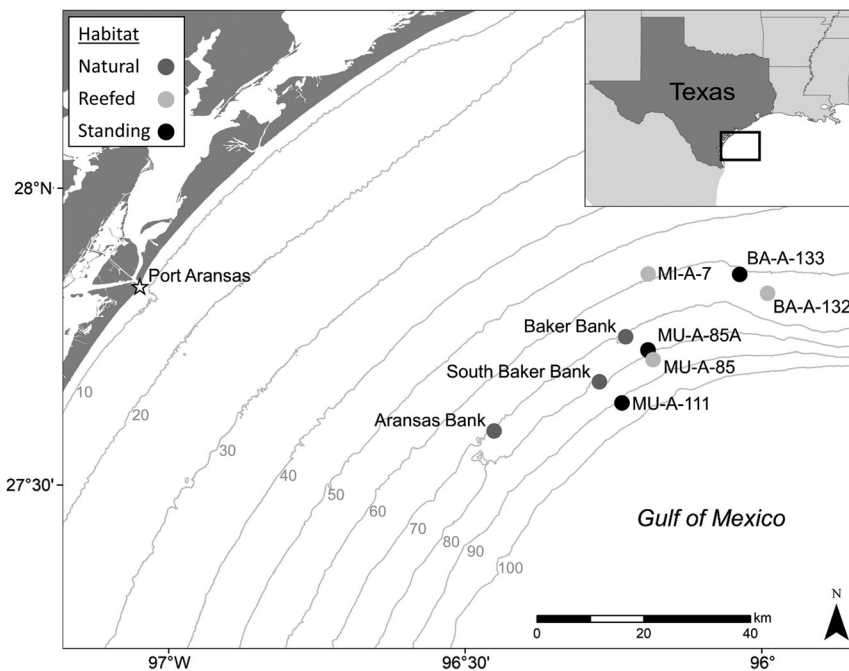For statistical analyses, red snapper were divided into 3 size classes based

Fig. 1. Study sites in the northwestern Gulf of Mexico, offshore of Port Aransas, TX showing 3 habitat types including natural reefs (Aransas Bank, Baker Bank, and South Baker), reefed platforms (BA-A-132, MI-A-7, and MU-A-85-A), and standing oil and gas platforms (BA-A-133, MU-A-111, and MU-A-85)

on the major trends observed in the relationship of stable carbon and nitrogen isotopes with total length: 'small' > 400 mm TL, 'medium' = 401 to 600 mm TL, and 'large' > 600 mm TL. Multivariate analyses of diet composition were conducted in PRIMER-6 on prey items grouped by LPT (see Table 1). Weight was converted to standardized prey weight by dividing each prey item by individual body weight of the fish to control for fish size in all multivariate analyses (Ajemian & Powers 2012). As such, only fish containing prey with a recorded body weight were considered in multivariate analyses. Using PRIMER-6, a Bray-Curtis similarity index was created with square root transformed, standardized prey weight (mg). Then, dispersion of prey within each year, habitat, and size class was assessed with permutational dispersion (PERMDISP) analyses. Afterward, this index was analyzed with permutational multivariate analysis of variance (PERMANOVA) to identify potential differences in diet by year, habitat, size class, and any interactions between these factors (Clarke 1993). Differences among factors (year, habitat, and size class) were then assessed using a similarity percentages (SIMPER) analysis of prey groups.

2.4. Stable isotope analysis

Muscle samples were stored in plastic bags and frozen until processing. Samples were defrosted on ice, rinsed briefly with DI water, and trimmed using a sterile scalpel or scissors to remove discoloration or connective tissue. Prepared samples were then placed in aluminum weigh boats and dried in a laboratory oven at 65°C for ~48 h until a constant weight was obtained. After drying, samples were homogenized with a mortar and pestle and stored in Whirl-paks®. Approximately 1 mg of powdered sample was loaded into tin capsules for analysis of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes. No lipid extractions were performed on tissue prior to stable isotope analysis based on previous red snapper studies (Wells et al. 2008, Zapp Sluis et al. 2013, Schwartz-kopf et al. 2017).

Elemental and isotopic compositions of carbon and nitrogen were determined by the Texas A&M University-Corpus Christi Isotope Core Lab using a Costech ECS4010 elemental analyzer connected to a continuous-flow Thermo Delta V Plus isotope ratio mass spectrometer via a Thermo Conflo IV interface. A multi-point calibration (Costech methionine standard: N = 9.39%; C = 40.25%) was used to determine carbon and nitrogen content of samples. Preliminary

isotopic values were measured relative to reference gases. Replicate analyses of isotopic standard reference materials USGS 40 ($\delta^{15}N$ = −4.52 ‰ AIR; $\delta^{13}C$ = −26.39 ‰ VPDB) and USGS 41 ($\delta^{15}N$ = 47.57 ‰ AIR; $\delta^{13}C$ = 37.63 ‰ VPDB) were used to normalize preliminary isotopic values to the AIR and VPDB scales (Paul et al. 2007). To ensure precision, all tissue samples were analyzed in duplicate and averaged before statistical analysis.

Exploratory data analysis was conducted in R v.3.5.1 (R Core Team 2013) and SigmaPlot 11. Relationships between fish length and stable isotope values were assessed using simple linear regressions on $\delta^{13}C$ and $\delta^{15}N$ with TL and SL. A simple linear regression was also conducted for $\delta^{15}N$ by $\delta^{13}C$. The nonlinear relationship and ontogenetic variations in $\delta^{13}C$ and $\delta^{15}N$ by habitat type were visualized using with a locally weighted smoothing (LOESS) curve (package ggplot2).

Variation in $\delta^{13}C$ and $\delta^{15}N$ between habitat and size class was assessed using a multivariate analysis of variance (MANOVA) in Minitab 18. The MANOVA design was Type III, full factorial with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables and habitat and size class as explanatory variables. Significant response variables identified from multivariate tests were followed with univariate analysis of variance (ANOVA). Post-hoc multiple comparisons with Tukey's honestly significant difference (HSD) test were then used to identify the source of variation within significant factors. Isotopic niche space based on the sample size corrected standard ellipse area (SEA_c) was calculated by habitat type and size class using the Stable Isotope Analysis in R (siar) and Stable Isotope Bayesian Ellipses (SIBER) packages in R (Parnell & Jackson 2003, Jackson et al. 2011). Significance was considered at α = 0.05 for all analyses.

3. RESULTS

3.1. Diet analyses

A total of 1585 red snapper were collected from natural reefs (n = 505), reefed platforms (n = 586), and standing platforms (n = 494). Fish ranged from 275 to 855 mm TL and 2 to 30 yr in age. There were 370 empty stomachs, 558 distended stomachs (also empty), and 657 containing prey (42.4% vacuity). Non-food items, including *Sargassum* spp. and plastic, were observed, but were uncommon, occurring in only 0.02% of the red snapper stomach contents. Unidentifiable prey was encountered in stomach

contents from all habitats ranging from 24.4% *W* at natural reefs, 25.5% *W* at standing platforms, to 29.9% *W* at reefed platforms. Identifiable prey from fish in the size range of 301 to 800 mm was obtained from 649 stomachs (212 natural reef, 214 reefed platforms, and 223 standing platforms), and only these fish were included in the analysis of diet composition among habitat types.

Of the 657 stomachs kept for examination of stomach contents, 155 were observed to have gastric parasites (23.6% infection). These trematode and nematode gastric parasites were observed in fish sized from 327 to 739 mm TL. Gastric parasite presence varied by habitat with natural reefs being highest (31.6% *N*), followed by reefed platforms (24.3% *N*), and standing platforms (14.8% *N*). The count of nematode parasites was fairly consistent between habitats (overall range = 11–14); however, trematode parasites exhibited greater variability. Natural reefs had the highest trematode parasite count (n = 57), followed by reefed platforms (n = 45), and standing platforms (n = 22). Parasite burden also varied by year with the highest rate of infection in 2015 (26.2% *N*), followed by 2013 (18.5% *N*), and 2014 (14.4% *N*). By year, nematodes varied greatly with the highest count in 2013 (n = 25), followed by 2014 (n = 13), and 2015 (n = 1). The trematode gastric parasites were also highest in 2013 (n = 55), followed by 2015 (n = 38), and 2014 (n = 31).

A total of 37 unique prey items were identified across all habitats. The species accumulation curves for all habitats combined reached an asymptote (*b* = 0.03), as did reefed platforms (*b* = 0.04). However, standing platforms (*b* = 0.05) and natural reefs (*b* = 0.05) were just below reaching an asymptote (Fig. 2). There were a total 28 prey taxa identified from natural reefs, 21 at reefed platforms, and 24 at standing platforms (Table 1). By weight, Osteichthyes (fish) made up the greatest percentage of the diet at all habitats, followed by Malacostraca (crustaceans). The third most common prey class at natural was Hydrozoa (siphonophores; 10.1% *W*), which also comprised a portion of the diet at standing platforms (2.72% *W*; Table 1). Cephalopoda was present in red snapper diet at standing (3.97%) and reefed platforms (2.18% *W*) as well as natural reefs (0.90% *W*; Fig. 3). The larger

sample size of individual prey items (%N) on natural reefs was driven by large quantities of very small gastropods and decapod crabs (Table 1). The remaining prey classes at all habitats made up <2% of the diet by weight (Table 1).

There were similarities in prey fish observed in red snapper diets between habitats. Some fish were present at all 3 habitats, such as Anguilliformes and Ophichthidae. The %*W* values varied by habitat, with reefed platforms having the highest percentage of both Anguilliformes (5.48%) and Ophichthidae (17.2%; Table 1). There were also prey fish that were only present at 2 of the 3 habitats, like Congridae and Carangidae, which were present in the diet at natural reefs and standing platforms (Table 1). Conversely, *Hoplunnis* spp. was only found in the diets from red snapper at reefed and standing platforms (Table 1). Some fish species were only documented at a single habitat. On natural reefs, this included whitebone porgy *Calamus leucosteus*, Clupeidae, and Haemulidae. The shrimp eel *Ophichthus gomesii* was unique to reefed platforms, while the pigfish *Orthopristis chrysoptera* and the wenchman *Pristipomoides aquilonaris* were unique to standing platforms (Table 1).

Within Malacostraca, numerous taxa were found in the diets across all habitats. These crustaceans included amphipoda, decapoda, isopoda, *Ogyrides* spp., the iridescent swimming crab *Portunus gibbesii*,
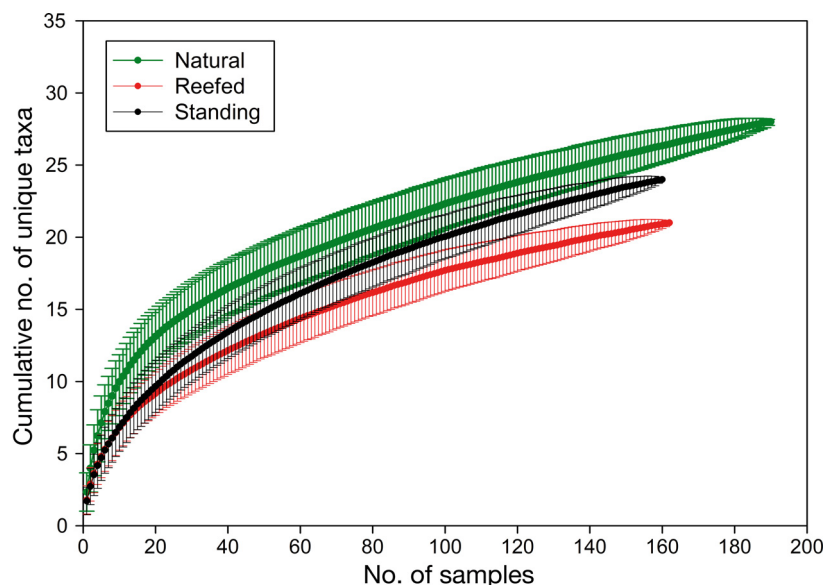

Fig. 2. Cumulative prey curves (mean ± SE) of unique prey taxa found in the diet of red snapper *Lutjanus campechanus* by number of specimens collected from natural reefs, reefed platforms, and standing oil and gas platforms in the western Gulf of Mexico

Table 1. Diet composition of red snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico by prey class and lowest possible taxon identified (LPT) showing percent frequency of occurrence, percent number, percent weight, and percent index of relative importance (% IRI) by habitat, including natural reefs (Nat, n = 226), reefed platforms (Reef, n = 215), and standing oil and gas platforms (Stand, n = 216); values in **bold** are totaled for prey class; empty cells represent non-detects

| Class/ Lowest possible taxon	Common name	%Occurrence Nat	Reef	Stand	%Number Nat	Reef	Stand	%Weight Nat	Reef	Stand	%IRI Nat	Reef	Stand
Bivalvia	Mollusk	**0.20**		**0.64**	**0.04**		**0.46**	**<0.01**		**0.01**	**<0.01**		**<0.01**
Cephalopoda	Cephalopod	**1.18**	**0.94**	**0.96**	**0.35**	**0.69**	**1.15**	**0.90**	**2.18**	**3.97**	**0.02**	**0.03**	**0.05**
Octopoda	Octopus	0.59			0.17			0.64			0.01		
Teuthida	Squid	0.59	0.94	0.96	0.17	0.69	1.15	0.25	2.18	3.97	<0.01	0.03	0.05
Gastropoda	Snails	**8.07**	**5.64**	**2.88**	**49.76**	**4.14**	**3.70**	**0.96**	**0.06**	**0.01**	**6.33**	**0.27**	**0.12**
Atlanta spp.	Heteropod	4.33	5.64	2.56	1.56	4.14	3.46	0.02	0.06	0.01	0.11	0.27	0.10
Cavolinia tridentata	Sea Butterfly	3.74			48.21			0.94			2.84		
Janthina janthina	Violet sea-snail			0.32			0.23			<0.01			<0.01
Hydrozoa/Siphonophora	Siphonophore	**3.35**		**1.92**	**0.73**		**1.39**	**10.11**		**2.72**	**0.56**		**0.09**
Malacostraca	Crustacean	**55.91**	**51.41**	**39.42**	**40.86**	**70.52**	**46.42**	**39.92**	**22.14**	**13.53**	**69.80**	**53.37**	**25.71**
Achelata	Lobster	0.20			0.04			0.01			<0.01		
Amphipoda	Amphipod	4.53	5.02	4.17	1.86	8.10	4.16	1.59	0.03	0.02	0.24	0.46	0.19
Decapoda	Unidentified decapod	8.66	6.27	5.45	20.02	7.24	4.62	4.40	0.80	3.35	3.27	0.57	0.47
Farfantepenaeus spp.	Penaeid shrimp	0.39	0.94		0.09	0.52		1.32	9.04		0.01	0.10	
Hippidae	Mole crab		0.31			0.17			0.28			<0.01	
Isopoda	Isopod	0.39	0.63	0.32	0.09	0.34	0.23	0.04	<0.01	<0.01	<0.01	<0.01	0.00
Malacostraca	Unidentified crustacean	15.94	10.66	11.54	3.72	6.21	8.31	9.72	4.96	5.96	3.31	1.33	1.79
Ogyrides spp.	Caridean shrimp	0.00	0.31	0.32		0.34	0.23		<0.01	<0.01		<0.01	<0.01
Portunus gibbesii	Iridescent swimming crab	0.39	0.31	0.32	0.22	0.17	0.46	0.88	0.90	0.77	0.01	<0.01	<0.01
Portunus spinicarpus	Longspine swimming crab	7.48	0.94	1.28	3.98	0.52	0.92	15.11	2.27	1.17	2.21	0.03	0.03
Portunus spinimanus	Blotched swimming crab	<0.01	0.31		<0.01	0.17			0.53	<0.01		<0.01	
Portunus spp.	Swimming crab	2.95	0.94	0.64	1.21	0.52	0.46	4.65	0.66	0.83	0.27	0.01	0.01
Speocarcinus lobatus	Gulf squareback crab	0.31			0.17			0.35			<0.01		
Stomatopoda	Mantis shrimp	14.76	24.45	15.38	9.60	46.03	27.02	2.21	2.32	1.43	2.70	13.25	4.76
Tanaidacea	Tanaid	0.20			0.04			<0.01			<0.01		
Osteichthyes	Fish	**28.15**	**41.38**	**53.85**	**6.92**	**24.31**	**46.65**	**46.29**	**75.62**	**79.76**	**23.15**	**46.33**	**74.03**
Anguilliformes	Eel	0.98	1.88	2.24	0.30	1.03	2.31	1.94	5.48	3.11	0.03	0.14	0.13
Calamus leucosteus	Whitebone porgy	0.20			0.04			2.63			0.01		
Carangidae	Jack	0.20		0.32	0.04		0.46	2.36		2.81	0.01		0.01
Clupeidae	Clupeid	0.20			0.04			0.20			<0.01		
Congridae	Garden eel	0.20		0.64	0.04		0.46	9.40		18.25	0.03		0.13
Haemulidae	Grunt	0.20			0.04			0.02			<0.01		
Hoplunnis spp.	Pike-Conger	<0.01	0.63	0.64		0.34	0.46		11.20	1.21		0.08	0.01
Ophichthidae	Snake-eels	0.79	0.94	0.64	0.17	0.52	0.46	7.94	17.20	5.76	0.10	0.19	0.04
Ophidiidae	Cusk-eels			0.64			0.46			0.05			0.01
Orthopristis chrysoptera	Pigfish			0.32			0.23			7.45			0.03
Osteichthyes (unidentified)	Unidentified fish	25.39	37.62	48.08	6.23	22.24	41.57	21.81	37.72	39.80	11.00	25.27	42.55
Pristipomoides aquilonaris	Wenchman			0.32			0.23			1.31			0.01
Ophichthus gomesii	Shrimp eel		0.31			0.17			4.03			0.01	
Ostracoda	Seed shrimp	**0.20**	**0.31**		**0.04**	**0.17**		**<0.01**	**<0.01**		**<0.01**	**<0.01**	
Polychaeta	Bristle worm	**0.20**	**0.31**		**0.04**	**0.17**		**<0.01**	**<0.01**		**<0.01**	**<0.01**	
Thaliacea	Salp	2.76		0.32	1.25		0.23	1.82		<0.01	0.13		<0.01
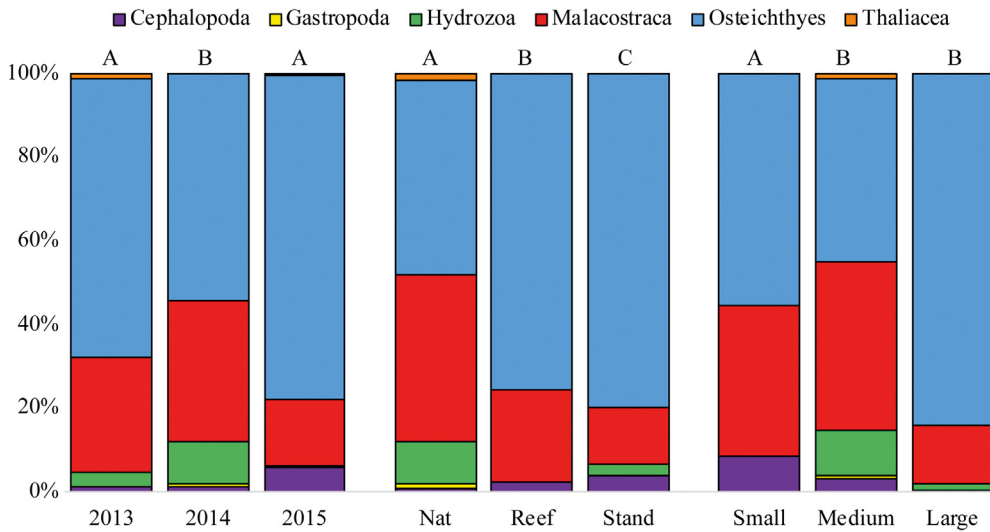
Fig. 3. Percent by weight (%W) of prey found in red snapper diet by year, habitat including natural reefs (Nat), reefed platforms (Reef), and standing oil and gas platforms (Stand), and size class (small: <400 mm TL, medium: 401–600 mm TL, and large: >600 mm TL) in the western Gulf of Mexico, excluding unidentified content and the following classes that made up <1% in any category (Bivalvia, Holothuroidea, Ostracoda, and Polychaeta); prey taxa are displayed as taxonomic class, and varied letters represent significant differences within each category

the longspine swimming crab *Portunus spinicarpus*, and mantis shrimp (stomatopoda; Table 1). The proportion of the diet represented by these crustaceans varied by habitat type. For example, decapod crabs had a higher % IRI value at natural (3.27%) than at reefed platforms (0.57%) or standing platforms (0.47%). The longspine swimming crab and unidentified swimming crabs also had higher % IRI at natural (2.21% and 0.27%, respectively), than at reefed platforms or standing platforms (both 0.03% and <0.01%; Table 1). Mantis shrimp were more important at reefed platforms (13.3% IRI) than at standing platforms (4.76% IRI) or natural reefs (2.70% IRI; Table 1.) Some crustaceans were only present at single habitat. Specifically, Achelata (lobster) and Tanaidacea were only found in the diet of red snapper at natural reefs with low importance (both <0.01% IRI; Table 1). Gulf squareback crab *Speocarcinus lobatus* (<0.01% IRI), blotched swimming crab *Portunus spinimanus* (<0.01% IRI), and mole crabs (Hippidae; <0.01% IRI) were unique to reefed platforms, but also with low importance (Table 1). No malacostracans were unique to standing platforms.

Other prey groups represented a smaller proportion of red snapper diet than fish and crustaceans. Gastropoda represented 6.33% IRI of the diet at natural reefs, with much less importance at reefed (0.27% IRI) and standing platforms (0.12% IRI; Table 1). Within Gastropoda, heteropods *Atlanta* spp. were found in the diet at all habitats (Table 1). Sea butterflies *Cavolinia tridentate* were unique to natural reefs and were consumed in very high quantities (48.2% *N*; Table 1), while the violet snail

Janthina janthina was unique to standing platforms (<0.01% IRI; Table 1). No gastropod was unique to reefed platforms. Cephalopods were found in the diet at all habitats, specifically squid (Teuthida). Octopus were only observed in the diet at natural reefs with low importance (0.01% IRI; Table 1). Bivalvia, Hydrozoa, and Thaliacea (salps) were present in the diet at natural reefs (<0.01%, 0.56%, and 0.13% IRI, respectively) and standing platforms in small quantities (<0.01%, 0.09%, and <0.01% IRI, respectively) but not at reefed platforms (Table 1).

There were significant interannual differences observed in red snapper diet dispersion (PERMDISP, $F_{2,508}$ = 8.32, p = 0.002) with 2015 having a different dispersion than 2013 or 2014. There was also annual variation in diet composition (PERMANOVA, Pseudo-F = 3.18, p = 0.001; Table 2). For example, diet in 2014 was significantly different than 2013 or

Table 2. Results from a 2-way crossed PERMANOVA on diet composition by prey class among habitat and size class (small: <400 mm TL, medium: 401–600 mm TL, large: >600 mm TL) of red snapper collected from natural reefs, reefed platforms, and standing oil and gas platforms in the northwestern Gulf of Mexico; df: degrees of freedom, SS: sum of squares, unique perms: unique permutations, values in **bold** are significant (p ≤ 0.05)

Factor	df	SS	Pseudo-F	p (perm)	Unique perms
Year	2	22290	3.18	**0.001**	997
Habitat	2	25858	3.68	**0.001**	997
Size class	2	14147	2.02	**0.007**	997
Habitat × Year	4	19165	1.37	**0.055**	998
Habitat × Size class	4	10482	0.75	0.885	998
Year × Size class	4	13980	1.00	0.479	999
Habitat × Size class × Year	8	25418	0.91	0.716	997

Table 3. Post-hoc pairwise comparisons of red snapper diet (n = 246) from the northwestern Gulf of Mexico by size class (see Table 2) and habitat (natural reefs, reefed platforms, and standing platforms); df: degrees of freedom, Unique perms: the number of unique permutations, values in **bold** are significant (p ≤ 0.05)

Factors	df	t	p (perm)	Unique perms
Year				
2013, 2014	381	2.20	**0.001**	996
2013, 2015	297	1.35	0.056	999
2014, 2015	290	1.83	**0.001**	999
Habitat				
Natural, Artificial	333	1.78	**0.001**	999
Natural, Standing	332	1.95	**0.001**	998
Artificial, Standing	303	1.51	**0.015**	999
Size				
Medium, Large	425	1.69	**0.004**	997
Medium, Small	374	1.15	0.196	999
Large, Small	169	1.09	0.287	998

2015 (Table 3). More fish were consumed in 2013 and 2015 than in 2014, where more crustaceans were consumed (Fig. 3). Other prey groups that drove differences by year included pelagic zooplankton, such as siphonophores and salps, and cephalopods, like squid and octopus (Table 1). The significant differences in diet observed between 2013 and 2014 is likely explained by higher percent contributions of Osteichthyes (0.43%) and Malacostraca (0.26%) in 2013, compared to more Stomatopoda (0.21%), *Portunus spinicarpus* (0.22%), and Siphonophora (0.13%) in 2014 (Table 4). The difference in diet between 2014 and 2015 was driven by much higher percent contributions of Osteichthyes in 2015 (0.65%) than in 2014 (0.39%; Table 4). Further, in 2015, there were also fewer crustaceans observed than in 2014 (Table 4).

The dietary dispersion of red snapper was significantly variable by habitat (PERMDISP, $F_{2,508}$ = 18.53, p = 0.001) with natural habitats having greater dispersion than either reefed or standing platforms. Diet composition was also variable by habitat (PERMANOVA, Pseudo-F = 3.68, p < 0.001; Table 2) with all habitats significantly different from each other (Table 3). Variation in the percent contributions of Osteichthyes, Malacostraca, Stomatopoda, Siphonophora, and *P. spinicarpus* accounted for the observed differences in diet among habitats (Table 4). Standing platforms had a higher contribution of Osteichthyes (0.61%) than reefed platforms (0.45%) or natural reefs (0.35%; Table 4). Diet at natural reefs had a higher proportion of Malacostraca (0.32%) than either standing (0.13%) or reefed platforms (0.11%; Table 4).

Stomatopoda was also higher at reefed platforms (0.13%) and natural reefs (0.11%), than standing platforms (0.08%; Table 4).

The dispersion of diet was not significant by size class (PERMDISP, $F_{2,508}$ = 0.764, p = 0.576); however, a significant effect of red snapper size class on diet composition was observed (PERMANOVA, Pseudo-F = 2.02, p = 0.007; Table 2). Specifically, the diet of the medium size class was significantly different than that of the large size class (Table 3). There was a greater percent contribution of Osteichthyes in the diet of large red snapper (0.58%) compared to medium (0.39%), but there was a greater contribution of Malacostraca observed in the diet of medium red snapper (0.21%) than that of large (0.08%; Table 4). In the diet of medium red snapper, Stomatopoda (0.11%), *Portunus spinicarpus* (0.14%), and Siphonophora (0.10%) were also a larger contribution to the diet than in the large size class (0.01%, 0.07%, and 0.05% respectively; Table 4).

3.2. Stable isotope analysis

A total of 712 muscle samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$; 251 from natural reefs, 228 from reefed platforms, and 233 from standing platforms. A positive relationship in isotopic space was observed between $\delta^{15}N$ and $\delta^{13}C$ for all habitats (r^2 = 0.62, $F_{1,710}$ = 1,151, p < 0.001). There was a weak linear relationship between $\delta^{15}N$ and TL (r^2 = 0.01, $F_{1,710}$ = 10.39, p = 0.001) and $\delta^{15}N$ and SL (r^2 = 0.01, $F_{1,710}$ = 8.80, p = 0.003) but not $\delta^{13}C$ and TL (r^2 < 0.01, $F_{1,710}$ = 0.84, p = 0.361) or $\delta^{13}C$ and SL (r^2 < 0.01, $F_{1,710}$ = 0.37, p = 0.545). The non-linear relationship of stable isotope values and TL was visualized with locally estimated scatterplot smoothing (LOESS) curve that revealed ontogenetically driven, habitat-specific trends. Red snapper from natural reefs were higher in both $\delta^{13}C$ and $\delta^{15}N$ in the smallest size classes, while standing platform values were highest for both isotopes in the large size class (Fig. 4). All habitats showed a decrease in both $\delta^{13}C$ and $\delta^{15}N$ in the 400 to 600 mm TL range; however, this was considerably less pronounced at standing platforms (Fig. 4). In the medium size class, natural reefs and reefed platforms had similar values for both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 4). In the large size class, standing platforms had the highest $\delta^{13}C$ and $\delta^{15}N$ values, while natural reefs and reefed platforms were slightly lower (Fig. 4). Overall mean $\delta^{15}N$ and $\delta^{13}C$ were highest at standing platforms (13.5 ± 0.04‰ and −17.8 ± 0.02‰), followed by natural reefs (13.2 ± 0.04‰ and −17.9 ± 0.02‰) and

Table 4. SIMPER analysis of red snapper diet (prey standardized weight by lowest possible taxon, n = 246) by habitat (natural reefs, reefed platforms, and standing platforms) and size class (see Table 2) collected from the northwestern Gulf of Mexico. Avg. diss.: average dissimilarity, SD: standard deviation, Cont. (%): contributing percent, Cumm. (%): cumulative percent

Taxon	Abundance		Avg. diss.	SD	Cont. (%)	Cumm. (%)
Year						
Average dissimilarity = 85.4	2013	2014				
Osteichthyes	0.43	0.39	25.1	0.96	29.4	29.4
Malacostraca	0.26	0.20	13.0	0.66	15.2	44.6
Stomatopoda	0.04	0.21	11.44	0.66	13.41	58.0
Portunus spinicarpus	0.11	0.22	7.04	0.39	8.25	66.3
Siphonophora	0.06	0.13	4.87	0.31	5.71	72.0
Average dissimilarity = 84.3	2014	2015				
Osteichthyes	0.39	0.65	29.6	1.10	35.2	35.2
Stomatopoda	0.21	0.05	10.8	0.67	12.8	48.0
Malacostraca	0.20	0.07	8.30	0.51	9.84	57.8
Decapoda	0.14	0.08	7.01	0.48	8.32	66.1
Portunus spinicarpus	0.22	0.03	6.24	0.35	7.40	73.5
Habitat						
Average dissimilarity = 86.7	Natural	Reefed				
Osteichthyes	0.35	0.45	24.84	0.95	28.67	28.67
Malacostraca	0.32	0.11	12.9	0.67	14.88	43.54
Stomatopoda	0.11	0.13	10.01	0.61	11.55	55.1
Portunus spinicarpus	0.30	0.04	7.85	0.40	9.06	64.15
Decapoda	0.11	0.04	5.09	0.40	5.88	70.03
Average dissimilarity = 85.7	Natural	Standing				
Osteichthyes	0.35	0.61	27.22	1.02	31.76	31.76
Malacostraca	0.32	0.13	13.16	0.67	15.36	47.13
Portunus spinicarpus	0.30	0.04	7.55	0.41	8.81	55.93
Stomatopoda	0.11	0.08	7.49	0.57	8.74	64.67
Siphonophora	0.16	0.05	5.35	0.33	6.25	70.92
Average dissimilarity = 79.7	Reefed	Standing				
Osteichthyes	0.45	0.61	34.71	1.24	43.58	43.58
Stomatopoda	0.13	0.08	10.9	0.64	13.68	57.25
Malacostraca	0.11	0.13	9.17	0.51	11.51	68.76
Decapoda	0.04	0.06	4.18	0.33	5.25	74.01
Size class						
Average dissimilarity = 84.5	Medium	Large				
Osteichthyes	0.39	0.58	30.26	1.07	35.81	35.8
Malacostraca	0.21	0.08	9.9	0.57	11.7	47.5
Stomatopoda	0.11	0.08	9.1	0.57	10.7	58.2
Portunus spinicarpus	0.14	0.07	5.09	0.33	6.03	64.2
Decapoda	0.07	0.07	4.47	0.37	5.29	69.5
Siphonophora	0.10	0.05	4.05	0.28	4.79	74.32

reefed platforms (13.0 ± 0.05‰ and −17.9 ± 0.02‰, respectively).

Both $\delta^{13}C$ and $\delta^{15}N$ of red snapper tissue significantly varied by habitat and size class (Fig. 5). A significant effect of habitat (MANOVA, $F_{2,4} = 17.36$, p < 0.001), size class (MANOVA, $F_{2,4} = 35.42$, p < 0.001), and year (MANOVA, $F_{1,2} = 43.78$, p < 0.001) on $\delta^{13}C$ and $\delta^{15}N$ values was observed with an interaction between size class and habitat (MANOVA, $F_{4,8} = 3.88$,

p < 0.001; Table 5). Subsequent univariate ANOVAs on habitat and size class showed that $\delta^{13}C$ varied by year (ANOVA, $F_{2,685} = 27.84$, p < 0.001) and size class (ANOVA, $F_{2,685} = 58.06$, p < 0.001), with a significant interaction between size class and habitat (ANOVA, $F_{4,685} = 5.27$, p = 0.006; Table 5). Post-hoc pairwise comparisons by habitat and size class revealed that $\delta^{13}C$ of fish tissue from standing and reefed platforms was higher than that from natural reefs for the largest size class (Fig. 6a). $\delta^{13}C$ was also significantly variable by year, with 2013 and 2014 higher than 2015 (Fig. 6b). $\delta^{15}N$ varied by year (ANOVA, $F_{2,685} = 15.86$, p < 0.001), habitat (ANOVA, $F_{2,685} = 13.04$, p < 0.001), and size class ($F_{2,685} = 26.18$, p < 0.001), with a significant interaction between size class and habitat (ANOVA, $F_{4,685} = 6.45$, p < 0.001; Table 5). For the medium and large size classes, fish from standing platforms were higher in $\delta^{15}N$ than those from both natural reefs and reefed platforms (Fig. 6c). $\delta^{15}N$ also varied significantly by year, with 2013 and 2014 higher than 2015 (Fig. 6d).

Variability in red snapper isotopic niche breadth was revealed by SIBER analyses (Fig. 7). Specifically, SEA_c was comparatively narrower in the small size class at all habitat types (Fig. 7). The small size class at natural reefs (0.17) had the smallest niche breadth of the study, followed by the small size class at reefed platforms (0.19; Fig. 7). For the small size classes, standing platforms had the widest niche (0.29). In the medium size class, niche space was generally much wider than in the small size class. The widest niche in the medium size class was at natural reefs (0.57), followed by reefed platforms (0.50) and then standing platforms (0.37; Fig. 7). For the large size class of red snapper, reefed platforms had the largest niche space by far (0.67), followed by natural reefs (0.35) and standing platforms (0.31; Fig. 7).
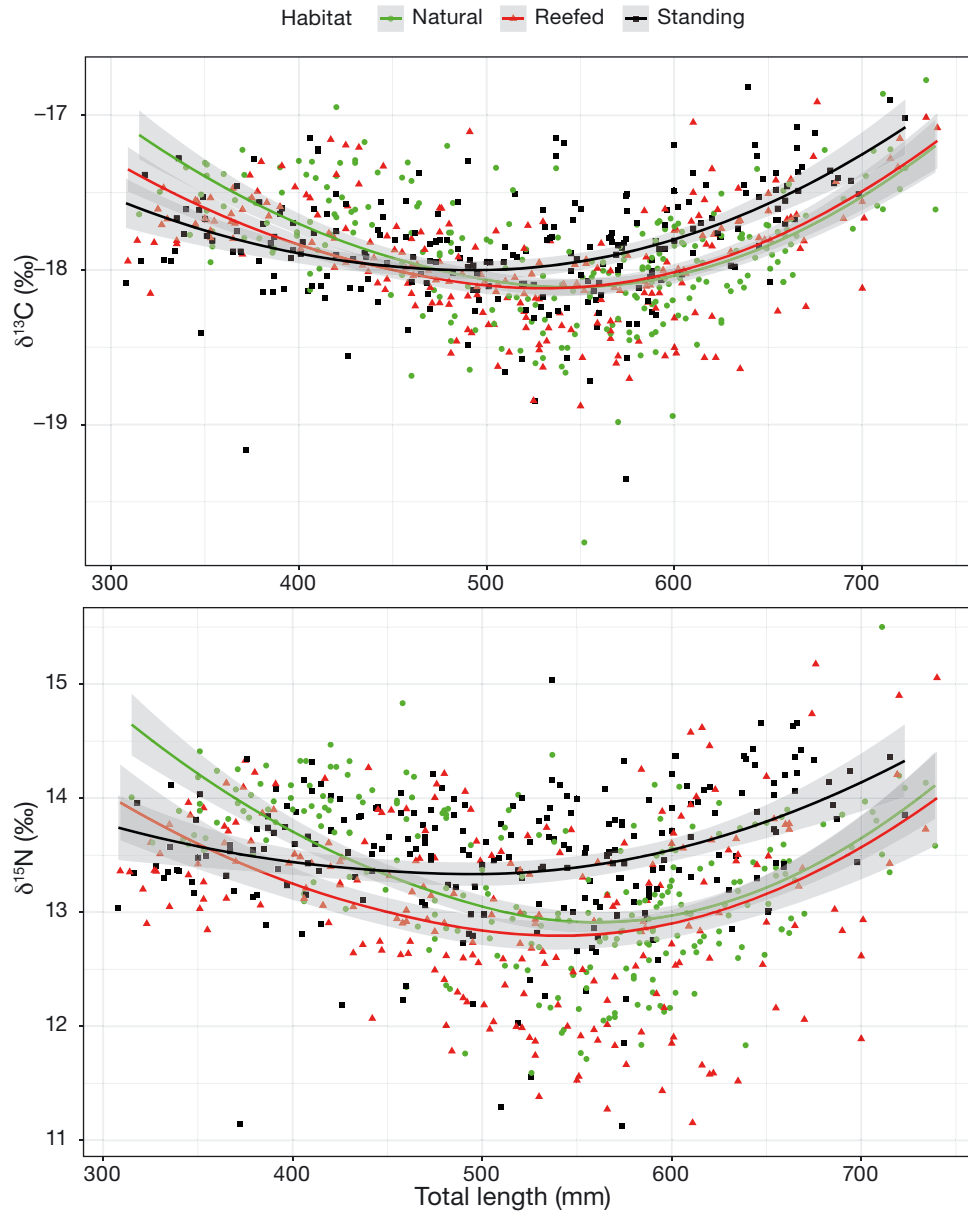
Fig. 4. Red snapper stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values and total length (TL) with local polynomial regression (LOESS) curve by habitat for natural reefs, reefed platforms, and standing oil and gas platforms; gray shading represents 95 % confidence intervals

4. DISCUSSION

Using robust sample sizes over multiple years, we found that there are significant annual and ontogenetic differences in in the trophic ecology of red snapper collected from natural reefs compared with those from reefed and standing. Further, this research documents a non-linear relationship of fish length and stable isotope values, confirming a mid-life (i.e. age 3 to 6; Streich et al. 2017b) decrease in trophic position for red snapper. Thus, the effect of habitat combined with ontogenetic variability may have certain ecological consequences for red snapper. Interannual variability in stable isotopes (both δ^{13}C and δ^{15}N) and diet was also observed, suggesting that environmental factors and fluctuations in prey availability are also influential to the trophic ecology of red snapper. As such, habitat-specific effects, and thus the ecological function of artificial habitats, may not be discernable without capturing a considerable ontogenetic or temporal range.
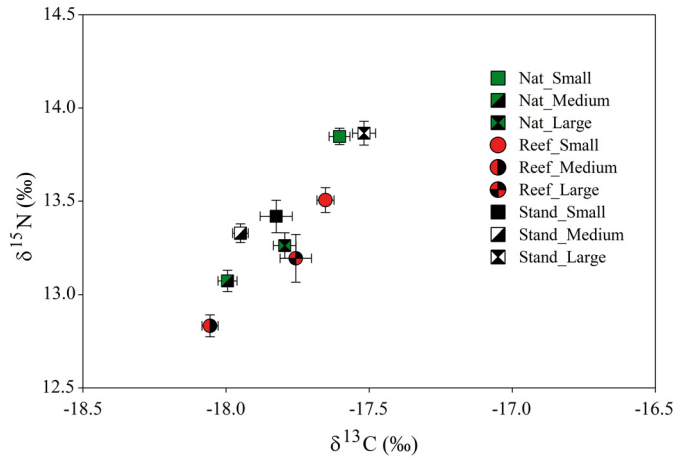
Fig. 5. Stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope values (mean ± SE) of red snapper by habitat, including natural reefs (Nat), reefed platforms (Reef), and standing oil and gas platforms (Stand), and size class (see Fig. 3)

Table 5. Multivariate analysis of variance (MANOVA) table comparing stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope values of red snapper by habitat (natural reefs, standing platforms, and reefed platforms) and size class (see Table 2) showing main effects and interactions with significance considered at $p \leq 0.05$ and individual univariate analysis of variance (ANOVA) for each factor showing individual response variables of δ^{13}C and δ^{15}N. SS: sum of squares, df: degrees of freedom; values in **bold** are significant

Factor	SS	df	*F*	p
MANOVA: δ^{13}C & δ^{15}N				
Habitat	NA	2,4	17.36	**<0.001**
Size class	NA	2,4	35.42	**<0.001**
Year	NA	1,2	43.78	**<0.001**
Habitat × Size class	NA	4,8	3.88	**<0.001**
Year × Size class	NA	2,4	0.29	0.883
Habitat × Year	NA	2,4	0.75	0.556
Habitat × Size class × Year	NA	4,8	0.53	0.833
ANOVA: δ^{13}C				
Habitat	0.28	2	1.45	0.235
Size class	11.06	2	58.06	**<0.001**
Year	5.30	2	27.84	**0.001**
Habitat × Size class	2.01	4	5.27	**0.006**
ANOVA: δ^{15}N				
Habitat	9.54	2	13.04	**<0.001**
Size class	18.98	2	26.18	**<0.001**
Year	11.49	2	15.86	**<0.001**
Habitat × Size class	9.35	4	6.45	**<0.001**

4.1. Diet

Diet of red snapper was variable by habitat, size class, and year, but none of these factors interacted statistically. This suggests that their diet is complex and inconsistent. Previous studies in the GOM have found adult red snapper to be generalist predators

(Bradley & Bryan 1975, Tarnecki & Patterson 2015, Foss 2016, Dance et al. 2018, Szedlmayer & Brewton 2019), and this research continues to support this notion. As suggested by Bradley & Bryan (1975), the diet of red snapper appears to be limited primarily by prey availability; therefore, a better understanding of this topic might provide more insight into red snapper trophic ecology.

Habitat-specific differences were observed in red snapper diet. Despite these observed differences among habitats, it is important to consider that the dispersion of diet by habitat was also significant. These differences in dispersion make the PERMANOVA results more difficult to interpret because it confounds habitat-related specificity of diet with dietary breadth (Clarke 1993). Based on stomach content and stable isotope analyses of intermediate sized fish, the relic coralgal, natural reefs supported a more diverse red snapper diet. This mirrors what has been found on salt dome reefs in the north-central GOM near Louisiana (Simonsen et al. 2015, Schwartzkopf et al. 2017). These corroborating studies reveal that multiple types of natural reefs support a broader prey base than do artificial habitats. Within artificial habitats, we also found that reefed platforms supported a more varied prey base than did standing platforms. It is possible that the change in orientation from vertical to horizontal allows red snapper access to more types of prey and that the lower relief of reefed platforms better mimics natural reef habitats.

The differences observed in gastric parasite burden between habitats also supports variation in diet by habitat. The highest percentage of infection was found on natural reefs, followed by reefed, then standing platforms. In particular, trematode parasites were found in higher quantities at natural reefs and reefed platforms than at standing platforms. This may indicate the prey item that is the host of this parasite is more readily available at natural reefs and reefed platforms. This further highlights the trophic similarities between these 2 lower relief habitats. Nematode gastric parasite burden was more consistent across habitats, which may indicate the prey item that transmits these parasites is cosmopolitan at all 3 habitats. Gastric parasites can be used as longer-lasting markers of trophic transfer (Locke et al. 2013); therefore, a comprehensive study of red snapper gastric parasite burden with molecular identification would allow for a better understanding of red snapper trophic ecology, especially considering the loss of prey items due to stomach eversion.

There was also a significant effect of size class on red snapper diet, confirming ontogenetic shifts iden-
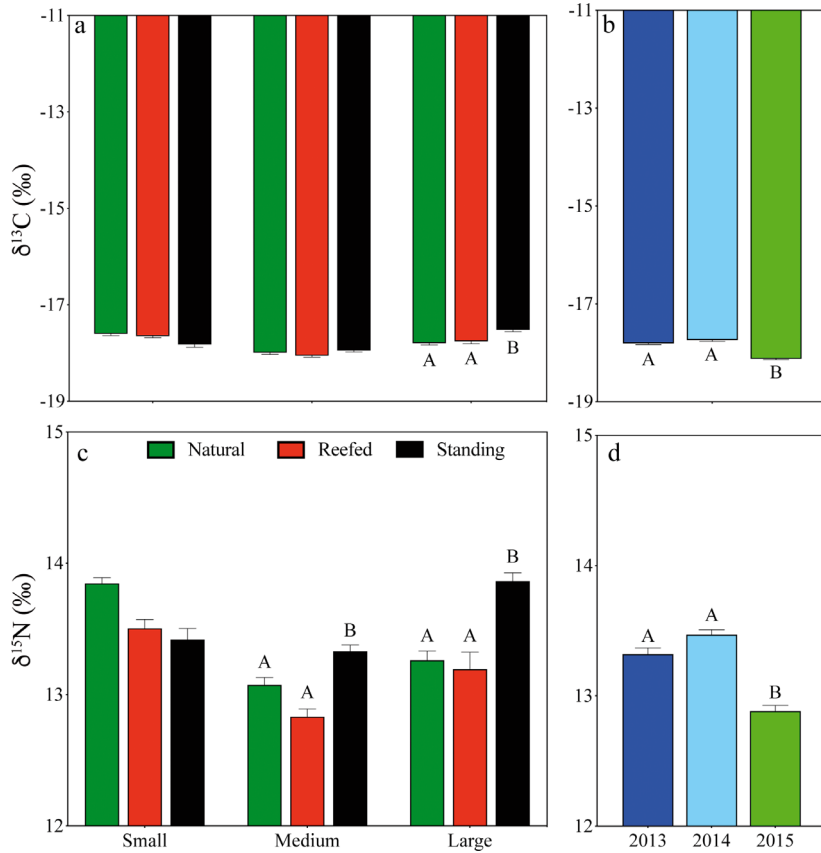
Fig. 6. Stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope values (mean ± SE) of red snapper by (a,c) size class (see Fig. 3) and habitat, including natural reefs, reefed platforms, and standing oil and gas platforms, and (b,d) year of collection; capital letters represent significant differences within a category

new prey groups may become available as TL increases. Significant differences occurred between the prey composition of the medium and large size classes, where we saw a decrease in crustaceans and an increase in fish. Interestingly, in the large size class, the prey was composed primarily of fish for all habitats, similar to observations for large red snapper in the north-central GOM (Schwartzkopf et al. 2017).

Annual variability in red snapper diets was also observed, with 2014 significantly different from 2013 and 2015; however, there were also significant effects observed in dispersion, which suggest caution must be taken in the interpretation of these data. These differences were primarily driven by the lower %W of prey fish and higher proportion of mantis shrimp and longspine swimming crabs in 2014. As red snapper are known to be opportunistic predators (Tarnecki & Patterson 2015, Foss 2016, Dance et al. 2018, Szedlmayer & Brewton 2019), their diet changes with prey availability. This is supported further by the gastric parasite abundance found in this study. For example, the number of nematode parasites observed was much lower in 2015 than in 2013 or 2014, which suggests that the host prey may have been less available that year. Thus, annual variability in prey populations is likely a driving factor in red snapper diets and could be further explored with concurrent sampling of invertebrates and small fishes at these sites.

tified in previous studies on smaller fish (Ouzts & Szedlmayer 2003, Szedlmayer & Lee 2004, Wells et al. 2008, Dance et al. 2018) as well as adults (Bradley & Bryan 1975, Tarnecki & Patterson 2015, Schwartzkopf et al. 2017). It is likely that feeding opportunities are variable by size class at each habitat and that
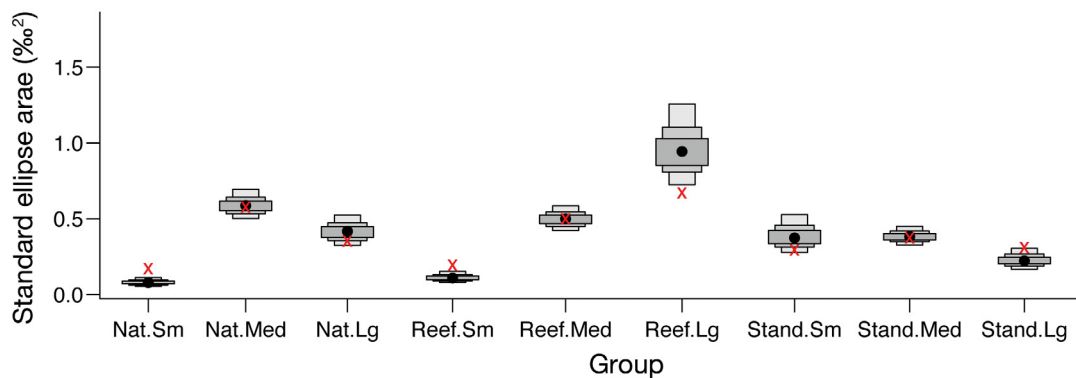

Fig. 7. Bayesian credible intervals by habitat, including natural reefs (Nat), reefed platforms (Reef), and standing oil and gas platforms (Stand), and size class (Sm: small; Med: medium; Lg: large; see Fig. 3); points represent the mean, boxes represent 50, 75, and 95 % credible intervals, and X's represent standard ellipse area corrected for sample size (SEAc)

This work also suggests that artificial habitats (i.e. reefed and standing platforms) may allow red snapper to take advantage of unique foraging opportunities in the GOM as prey items unique to these habitats were identified. This supports similar findings in the North Sea wherein platform habitats provided unique prey for multiple fish species (Fujii 2016). Habitat-specific prey observed in diets during this study included fish, such as Ophidiidae and *O. chrysoptera* on standing platforms and *S. lobatus*, *P. spinimanus*, and *Hippidae* sp. on reefed platforms. There were also crustaceans that were unique to reefed platforms, including Gulf squareback crab *Speocarcinus lobatus*, blotched swimming crab *Portunus spinimanus*, and mole crabs. At standing platforms, the violet snail *Janthina janthina* was another habitat-specific prey item. These habitat-specific prey may provide red snapper with alternative food sources during fluctuations in prey availability.

It is also important to note that some taxa are easier to identify due to persistent hard structures, such as Portunidae, Carangidae, Stomatopoda, and Cavoliniidae, which may have inflated the importance of these taxa to the diet of red snapper. Furthermore, the loss of an unknown amount of prey due to stomach eversion during collection from considerable depths suggests we could not have obtained a complete record of all prey items. While the cumulative prey curves suggest there was enough identifiable prey to accurately describe the diet, the slope of lines created by the last 4 points on the cumulative prey curves for standing and natural habitats were not asymptotic. This suggests that more samples might yield more prey species and more comprehensive understanding of red snapper diet.

The majority of fish prey for all habitats were unidentifiable due to advanced decomposition. This issue is common in red snapper diet studies, with many studies reporting a large proportion of the diet as unidentified fish (Bradley & Bryan 1975, Szedlmayer & Lee 2004, McCawley & Cowan 2007, Simonsen et al. 2015, Tarnecki & Patterson 2015, Foss 2016, Dance et al. 2018). The addition of DNA barcoding or other molecular identification techniques would be useful in ascertaining fine-scale differences in diet between habitats and in removing some of the bias due to the easily identifiable features of some taxa (Valdez-Moreno et al. 2012, Côté et al. 2013, Foss 2016, Spanik 2018, Szedlmayer & Brewton 2019). The identification of more fish to species would also allow for better understanding of the relative importance of reef-associated prey in red snapper diets (Szedlmayer & Brewton 2019). Such techniques are therefore suggested for future studies requiring species-level taxonomic discrimination of prey items.

4.2. Stable isotopes

Some previous research in the northern GOM has found a linear relationship between red snapper length and $\delta^{15}N$ values allowing for a length-correction to be applied to isotope values (Wells et al. 2008, Zapp Sluis et al. 2013, Simonsen et al. 2015, Tarnecki & Patterson 2015, Foss 2016). Similar positive relationships between size and stable nitrogen isotope values have also been found for other marine fish, such as summer flounder *Paralichthys dentatus* (Buchheister & Latour 2011), cape hakes *Merluccius capensis* and *M. paradoxus* (Van Der Lingen & Miller 2014), and red lionfish *Pterois volitans* (Dahl & Patterson 2014). Interestingly, we did not observe a strong linear relationship between fish size and carbon or nitrogen stable isotopes. However, based on the LOESS curve, a non-linear ontogenetic trend was present at all habitats. In this study, diet was most diverse for all habitats in the medium size class, which may explain the observed reduction in $\delta^{15}N$ as lower-level trophic organisms composed a greater portion of the diet in these size classes. A similar decrease was found in the north-central GOM for red snapper in the ≥400 TL size classes (Tarnecki & Patterson 2015). The larger sample size in our study (712 vs. 65) facilitated greater exploration of this trend throughout ontogeny, but especially for larger red snapper (>600 mm TL). Decreases in red snapper trophic position with size has been associated with an increase in zooplankton consumption (Tarnecki & Patterson 2015), which does align with findings from this study. For example, in the medium size class, there was a higher %*W* of Hydrozoa and Thaliacea; however, the amount of zooplankton reported by Tarnecki & Patterson (2015) was much higher (~50% *W* dry), than in this study (~10% *W* wet). In addition, the lowest $\delta^{13}C$ values were observed at natural reefs and reefed platforms in the medium size class. These decreased $\delta^{13}C$ values have been interpreted as representing a greater planktonic contribution to the diet (Schwartzkopf et al. 2017).

The SEAc is a measure of the total amount of niche space occupied (Jackson et al. 2011). Interestingly, higher SEAc was found in the medium size class at natural reefs and reefed platforms, where the trophic decrease was observed. The greatest SEAc was observed for large red snapper at reefed platforms, which indicates the trophic diversity of the diet in this

size class was greatest. This diet diversity may be due to the unique structure of artificial reefs that combine characteristics of standing platforms and natural low-relief habitats for foraging. Further, this wider trophic breadth may help explain the higher growth rates observed beyond Age 6 at reefed platforms for this same collection of fish (Streich et al. 2017b). It is worth considering that this size class also had the greatest representation in this study, which could have affected results.

It appears that standing platforms may provide a more consistent, higher trophic level food resource throughout ontogeny. This may be an effect of the high species richness observed on standing platforms (Ajemian et al. 2015) or an extended daily feeding period due to artificial light (Foss 2016). This enrichment could also represent less access to lower trophic level prey. Nitrogen enrichment, such as this, has been associated with higher total mercury tissue burden (Bank et al. 2007, Zapp Sluis et al. 2013), which is a consideration for fish and human health. Foss (2016) showed similar trends in nitrogen isotope values at standing platforms, which were characterized as having higher amounts of light driving the growth of primary producers, such as macroalgae. Furthermore, the sessile communities on platforms vary by depth, and algal abundance is higher near the surface in offshore waters (Lewbel et al. 1987), which could account for some of the variation between low- and high-relief habitats. Our finding of higher $\delta^{15}N$ values on red snapper from standing platforms for the large size class (>600 mm TL), which represent approximately Age 5+ fish (Streich et al. 2017b), is consistent with the other habitat-specific trophic studies from the Gulf of Mexico region (Simonsen et al. 2015, Schwartzkopf et al. 2017).

Red snapper from standing platforms collected during this study had more spawns per season (19.0), as opposed to natural sites (15.2) and reefed platforms (14.7; Downey et al. 2018). Other reproductive characteristics, including batch fecundity and annual fecundity, were also higher at standing platforms, though not significantly different from reefed and natural reefs (Downey et al. 2018). The combination of higher $\delta^{15}N$ values and increased reproductive potential for red snapper on standing platforms seems to indicate a slight enhancement for these fish relative to other habitats. However, the ecological implications of this enrichment and potential synergistic effects of fishing pressure on reproductive behavior warrant further study.

The higher $\delta^{15}N$ at standing platforms could also be an effect of food web alteration or contamination with hydrocarbons seeping from the production rig. There are documented effects of contaminants from oil and gas platforms on the epifaunal prey community (Peterson et al. 1996). Variation in epifaunal communities near platforms leaching contaminants into the water or sediment could have bottom-up effects on the localized food web, thus resulting in varied isotopic signatures in red snapper at different sites within the same habitat. This could be investigated further by assessing the chemical burden of water and sediments from these sites or by testing for a molecular response of cytochrome P450 induction, which is expressed by fish during the metabolism of hydrocarbons (Goksøyr 1995, Brewton et al. 2013). Future work should assess the water quality, physical parameters, and biogeochemical ecology of natural and artificial reefs in the GOM to understand what else may be contributing to these differences.

Significant interannual variability was observed in red snapper stable isotope values. For example, red snapper collected in 2015 had significantly different stable isotope signatures (both $\delta^{13}C$ and $\delta^{15}N$) than fish from 2013 and 2014. An explanation for these changes may be found in the significant increase in rainfall during the study. During the sampling events of 2013 and 2014, Texas was in extreme drought conditions that began in 2010. A very wet year began in winter 2014 (https://www.ncdc.noaa.gov/), and then the last season of sampling was in summer 2015. It is possible that this environmental variability may have affected the basal nutritional sources of red snapper. As extreme rain events are predicted to increase due to climate change, annual variability in stable isotopes may also increase due to fluctuations in nutrient loading. For example, riverine nitrogen loading is expected to increase ~20% by the end of the 21st century (Sinha et al. 2017), which could add to variability in downstream, even offshore, stable isotope signatures. Though not observed in our diet data, the lower $\delta^{13}C$ values in 2015 may be an effect of greater zooplankton contribution to the food web (Schwartzkopf et al. 2017), due to an increase in phytoplankton abundance via higher nutrient availability. The $\delta^{15}N$ for red snapper was also significantly lower in 2015, suggesting that lower trophic level organisms may have composed a higher proportion of their diet in that year.

A lack of long-term residency on a site or habitat type could also help explain the variation in observed trophic ecology among these offshore habitats. For example, large red snapper may move between natural and reefed platforms throughout the course of a day or can be motivated to relocate by seasonal

changes in temperature (Topping & Szedlmayer 2011, Piraino & Szedlmayer 2014, Williams-Grove & Szedlmayer 2016). These movements might lessen or obscure isotopic differences between habitats. Furthermore, recent studies using fine-scale tracking methods show red snapper move on and off structure, with 77% of tagged fish occupying a secondary habitat (Williams-Grove & Szedlmayer 2016). Thus, due to the proximity of some sites, it is possible that red snapper may be moving between the natural and artificial reef sites used in this study. Large red snapper tagged in the study region at sites <40 m have been shown to have movement ranges of from 2.74 to 13.1 km (Curtis 2014), making the prospect of traversing our study sites (range 2 to 52 km) feasible for the larger size classes where $\delta^{15}N$ or $\delta^{13}C$ was similar among habitats.

4.3. Management and conservation implications

This collection of red snapper from natural and artificial reefs in the western GOM displayed significant differences in trophic ecology, as well as growth (Streich et al. 2017b), but not reproductive potential (Downey et al. 2018). The variability in different aspects of their biology makes interpretation of these respective habitat values difficult. Despite this challenge, red snapper from reefed platforms had trophic similarities to those from natural reefs at certain sizes, and these reefed platforms also supported the fastest-growing fish (Streich et al. 2017b) with similar reproductive potential (Downey et al. 2018). These data combined suggest that reefed platforms may be an effective strategy for creating additional habitat for this important species. For example, the diet diversity observed at reefed platforms in this study may translate into faster growth (Streich et al. 2017b). Habitat has been cited as one possible limiting factor for red snapper populations (Shipp & Bortone 2009); thus, converting some decommissioned oil and gas platforms into artificial reefs may be beneficial as fishery managers strive to rebuild the GOM stock. Due to their conspicuousness on bottom sounders, and thus ease of identification by boat captains, artificial reefs can also direct fishing pressure away from natural reefs, which may help to preserve these habitats. The results of this study have implications for management, as there are currently hundreds of oil and gas platforms off the Gulf coast approaching decommissioning and removal. Given the apparent suitability of reefed platforms to serve as red snapper habitat, it may be prudent to retain some of these upright plat-

form jackets as artificial reefs. Globally, RTR programs are being developed to help develop environmentally sound choices for the management of decommissioned rigs. This study suggests that for one reef-associated fish species, reefed platforms can provide suitable habitat with sufficient trophic resources to support its biological and ecological needs.

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