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Evaluation of red snapper *Lutjanus campechanus* trophic dynamics with simultaneous stomach content and stable isotope analysis

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ABSTRACT: The importance of multiple prey taxa to red snapper *Lutjanus campechanus* diet was investigated using simultaneous stomach content analysis (SCA) and stable isotope analysis (SIA) over a 2 yr period in the north-central Gulf of Mexico (GOM) across 3 depth strata and 3 artificial structure types. Stable nitrogen isotope values were also used to estimate the trophic positions (TPs) of red snapper and prey items. SCA results showed that a variety of taxonomic prey groups were consumed, but the most frequent prey were stomatopods, portunid crabs and several families of fish. Some isotopic differences were found between red snapper size and age classes and across habitat types and depth strata for each sampling year; however, no consistent differences were found across the entire study period. Stable isotope mixing model results showed that diet varied annually, with sciaenid fishes being the greatest contributor in 2016 and portunid crabs in 2017, with the remaining proportions split across other taxa. Red snapper TP ranged from 3.4 to 4.8, while that of most prey groups was highly variable. The consistency in red snapper isotope values and the isotopic inconsistency of prey groups suggests that individual red snapper feed evenly across a taxonomically and isotopically diverse prey field. These results help develop a better understanding of reef ecology and food web structure in the northern GOM. Future investigations of red snapper diet that characterize reef habitats in terms of the available prey field and environmental conditions would improve our understanding of its trophic role in reef food webs.

KEY WORDS: *Lutjanus campechanus* · Stomach content analysis · Stable isotopes · Food webs · Gulf of Mexico

1. INTRODUCTION

The approach for fisheries management worldwide is shifting from single species to ecosystem-based fisheries management (EBFM), which attempts to incorporate linkages between multiple species and various ecosystem elements (Pikitch et al. 2004). This holistic approach is more adaptative than traditional management strategies, as it considers multiple species objectives and linkages to various ecosystem drivers. These can include factors such as habitat quality, fishing pressure, and drivers of recruitment and trophic connectivity, which all may vary spatially and temporally (Christensen et al. 1996, Thomas & Huke 1996, NRC 1999, Arkema et al. 2006). Quantifying trophic connections is crucial for the shift to

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multi-species fisheries management, because predator–prey interactions can influence fish population mortality more than fishing pressure alone (Christensen & Pauly 2004). While EBFM has great potential to allow fisheries managers to predict and respond to impacts from multiple stressors on targeted fish populations, the data needs for these management plans are high and data are often lacking. Trophic connections are most often gleaned from stomach content analysis (SCA), which provides valuable diet data but has inherent shortfalls which limit its ability to provide quantitative data required for the development of EBFM models (Buckland et al. 2017, Amundsen & Sánchez-Hernández 2019). A better understanding of the trophic interactions of commercially important species is essential to better assess the effects of fishing pressure and ecosystem alterations on stocks (Longo et al. 2015).

Traditional SCA can be complemented with stable isotope analysis (SIA) to identify basal resources and examine food web structure and trophic linkages, which can aid in the development of EBFM food web models and are particularly useful when prey items are not available or cannot be easily identified (McClain-Counts et al. 2017). Stable isotopes are integrated natural tracers that provide information on longer-term dietary patterns than SCA alone (Fry 2006). The stable isotope values of consumers are dependent upon the isotopic mixing of food sources and isotope fractionation during biochemical reactions (Peterson & Fry 1987). The stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are commonly measured in food web studies due to the ease of measurement and the complementary information they provide. Carbon experiences minimal isotopic fractionation resulting in consumer $\delta^{13}C$ values that reflect basal resource contributions (Fry 1983, Peterson 1999), while nitrogen exhibits larger trophic isotopic fractionation, resulting in predictably higher consumer $\delta^{15}N$ relative their food source (Minagawa & Wada 1984, Post 2002, Fry 2006). Stable isotope mixing models use isotope values of consumers and prey to estimate relative contributions of prey types to the diet of a consumer.

Red snapper *Lutjanus campechanus* is a structure-associated fish that has high economic and recreational value throughout its geographic range in the western Atlantic Ocean, extending from the Amazon River delta to Cape Hatteras, North Carolina (USA), including the Gulf of Mexico (GOM) (Wilson & Nieland 2001). Juveniles undergo ontogenetic shifts in habitat and diet upon reaching maturity at about 2 yr of age when they migrate from less complex shallow-water habitats to larger offshore structures. During this time, their diets shift from smaller prey, such as zooplankton and mysid shrimp, to larger prey items including various crustaceans and fishes (Wilson & Nieland 2001, Szedlmayer & Lee 2004, Dance & Rooker 2019). Once adults settle on reef habitats, they exhibit high site fidelity, generally staying within 500 m of their home structure (Schroepfer & Szedlmayer 2006, Gallaway et al. 2009); however, red snapper do stray from structures to feed on benthic and pelagic prey, which transfers energy and nutrients subsides back to reef habitats (McCawley & Cowan 2007). Red snapper have not been shown to exhibit a preference between artificial and natural reefs, but individuals on artificial reefs consume less diverse prey than those on natural reefs (Tarnecki & Patterson 2015, Schwartzkopf et al. 2017). Few natural reefs exist offshore of Mississippi (USA), so the majority of red snapper here utilize artificial reefs and abundant petrochemical platforms. However, information regarding the trophic ecology of red snapper in these waters is lacking.

Many studies have used SCA and SIA to investigate the feeding habits and trophic ecology of red snapper over various temporal and spatial scales in the northern GOM, but few have been able to examine red snapper diet over longer time scales. Knowledge of spatiotemporal variability of feeding habits and trophic ecology of this species inhabiting reef structures in Mississippi waters can inform EBFM plans. In addition, most studies examine prey items at broad taxonomic levels due to the inherent difficulties in visually identifying partially digested prey. Genetic identification allows for a finer taxonomic resolution that can confirm visual identifications as well as identify unknown prey items, which can improve our understanding of red snapper trophic dynamics. Our primary objective was to use simultaneous SCA (visual and genetic identification) and SIA to investigate the importance of multiple prey taxa to red snapper diet. We also estimated the trophic positions of red snapper and prey items using $\delta^{15}N$ values, with particulate organic matter (POM) as an isotopic proxy for the food web base (Wells et al. 2008, Dance et al. 2018).

2. MATERIALS AND METHODS

2.1. Sampling area and timeframe

Red snapper were collected monthly from April through October 2016–2017 from 23 sampling sites off Mississippi in the north-central GOM (Fig. 1).

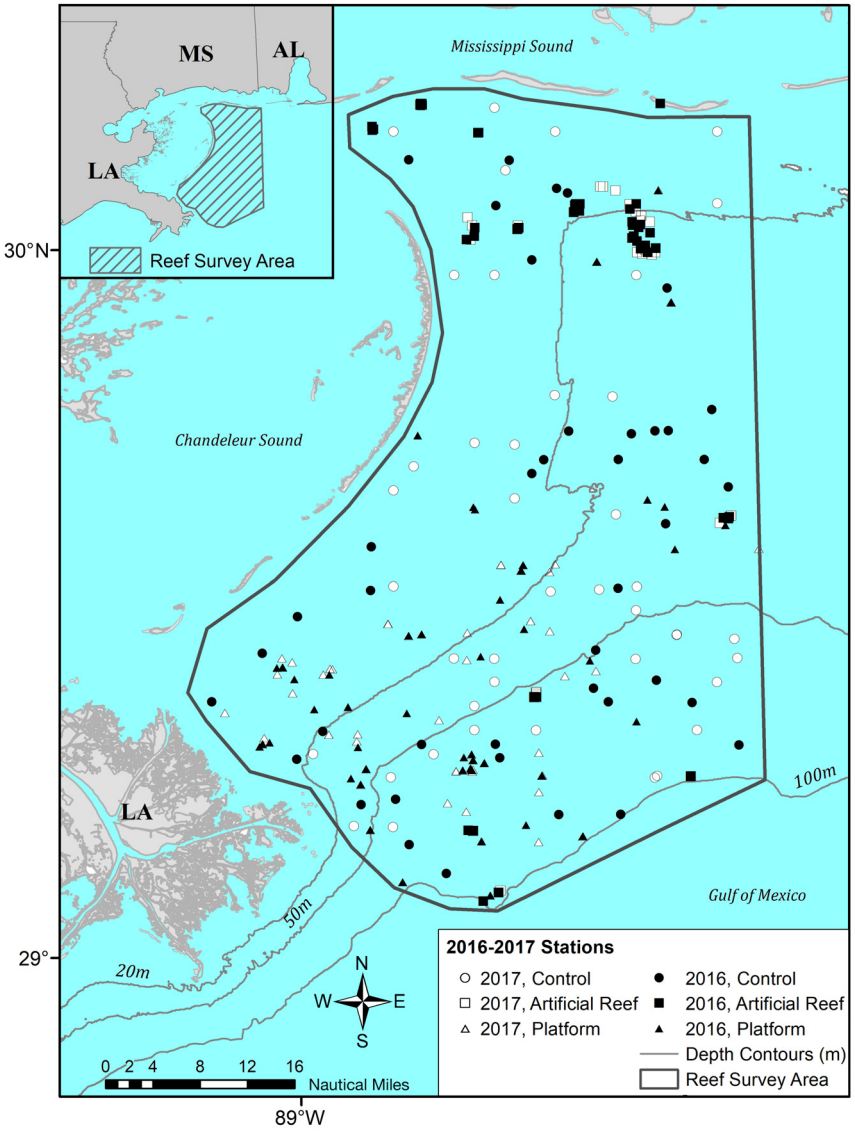

Fig. 1. Sampling effort in 2016 and 2017. Locations for 2016 and 2017 are marked by symbols denoting structure type. LA: Louisiana, MS: Mississippi, AL: Alabama

Monthly sites were selected from 3 depth strata (shallow: 0–20 m, mid: 21–50 m, deep: 51–100 m) and 3 structure types (non-structured controls, artificial reefs and active petroleum platforms) using a stratified random design. Artificial reef structure types included constructed 'fish havens' and 'Rigs-to-Reefs' (R2R). Offshore fish havens range in size from 3 to 4000 ha and are composed of large concrete slabs and culverts, steel hull vessels and other types of fabricated structures. R2R sites are decommissioned petrochemical platforms toppled in place, towed to specific locations or partially removed from a site, leaving a portion of the structure base in accordance with the National Artificial Reef Plan (NOAA 2007). Monthly sampling sites consisted of 3 fish haven reefs for the shallow and mid strata and 2 R2Rs for the deep stratum where no fish havens exist (8 artificial reef sites); 3 petroleum platforms in each stratum (9 platform sites); and 2 bare-bottom, no-structure control sites in each stratum (6 control sites). Most petroleum platforms sampled were in the southern portion of the sampling region across the 3 depth strata (Fig. 1).

2.2. Red snapper and prey collection and processing

Red snapper specimens at each site were collected following the NOAA Southeast Area Monitoring and Assessment Program Vertical Line Survey Protocol, Version 1.7 (Rester 2015) using 3 electric bandit reels deployed for 5 min. To target a broad size range of fish, each reel was rigged with 10 hooks of a particular size (8/0, 11/0, 15/0) spaced ~61 cm (24 inches) apart for a total of 30 hooks per site. Fishing lines were deployed to within 1.5 m of the top of artificial reefs or above the bottom near active platforms and at control sites. Once captured, individual red snapper were marked with a unique tag number and immediately stored on ice. Biometric parameters (total length, standard length, fork length, total weight, sex) were recorded for each fish within 24 h of capture. Stomachs were excised, placed in labeled Whirl-Pak bags and frozen/stored at −20°C. Muscle samples (~6 cm^3) were collected from the dorsal area of each fish, placed in labeled Whirl-Pak bags and frozen at −20°C until they were prepared for SIA. Both sagittal otoliths were removed when possible; one was used for age assessment and the other was archived. Otolith processing and ageing methodologies followed guidelines provided by VanderKooy et al. (2020). Otolith annuli counts were conducted by 3 experienced, independent readers and consensus was reached on final ages.

Prior to SCA, thawed stomach contents were rinsed over a 500 µm sieve. In addition to SCA prey items, 4 gobies in 2016 were regurgitated by red snapper due

to barotrauma when the fish were pulled on deck and hence were not included in SCA but were analyzed for stable isotopes values. Prey items were morphologically identified to the lowest possible taxonomic level using published scientific literature and identification guides (Fahay 1983, Williams 1984, McEachran & Fechhelm 1998, 2006, Carpenter 2002a,b, Richards 2005). Morphologically unidentifiable prey samples that had sufficient tissue (~1 cm^3) were refrozen until processed for DNA barcoding (Handy et al. 2011). Samples for barcoding were placed on a clean petri dish and cored (2–3 mm^3) with flame-sterilized forceps and scalpels to remove tissue that may have been contaminated by the stomach lining and/or gastric fluids. DNA from each sample was extracted using a commercial kit (DNeasy Blood and Tissue Kit; Qiagen). The ~650 bp barcode region of cytochrome C oxidase subunit I (COI) was amplified and then visualized on a 2% agarose gel, and positive reactions were sent to Eurofins for PCR clean-up and single-read sequencing. Sequences were trimmed using CLC Main Workbench to remove ambiguous and/or low-quality sequences and primer sequences. DNA barcode sequences were analyzed using the Barcode of Life Data System (BOLD) and/or NCBI BLAST to identify the closest match(es) to known COI sequences. The closest match was identified based on a sequence similarity of at least 99% and >500 bp for species, 95–99% and >500 bp for genus and <95% and >500 bp or >95% and 300–500 bp for family. Any prey material identified visually or that remained after the DNA barcoding procedure was refrozen until prepared for SIA.

We present SCA data both as percent weight (%W, wet weight of each prey type divided by the total wet weight of prey) and percent frequency of occurrence (%FO, proportion of individuals with non-empty stomachs containing a particular prey type) The %FO has been shown to provide the most detailed information about the diversity and availability of prey (Ahlbeck et al. 2012, Baker et al. 2014, Buckland et al. 2017, Amundsen & Sánchez-Hernández 2019); however, %W better reflects the importance of prey for consumers and is more compatible with stable isotope mixing model results. To be consistent with and allow comparisons to be made with the annual isotope mixing model results, cumulative annual %W and %FO are presented herein.

2.3. SIA of red snapper and prey items

All frozen samples were lyophilized for 48 h, ground to a fine powder with a mortar and pestle and then stored in 20 ml scintillation vials with polypropylene cone caps in desiccator cabinets. For the 2016 and 2017 collections, 220 and 136 prey items, respectively, were available for SIA. A subsample of each crustacean prey sample was acid-washed with 10% HCl to remove carbonates associated with the carapace (Carabel et al. 2006), centrifuged at 500 rpm for 5 min and rinsed with deionized water. Samples were then centrifuged, decanted 3 times and then frozen and freeze dried. Subsamples of all dried tissues (0.3–1 mg) were packed into tin capsules and analyzed in duplicate for %C, %N, $\delta^{13}C$ and $\delta^{15}N$ at the University of Southern Mississippi Gulf Coast Research Laboratory with a Thermo Finnegan Delta V Advantage stable isotope ratio mass spectrometer coupled to a Costech 4010 elemental analyzer via a Thermo Conflo IV interface. For acid-washed prey samples, we present the acid-treated $\delta^{13}C$ and the non-treated $\delta^{15}N$, as acid washing can affect the latter (Bunn et. al., 1995). The C:N ratios of red snapper tissue samples were all <3.5, indicating low lipid content (Logan et al. 2008), but $\delta^{13}C$ for fish prey items with C:N ratios above this threshold were mathematically lipid corrected according to Post et al. (2007):

$$\Delta\ \delta^{13}C = -3.32 + 0.99 \times C{:}N \quad (1)$$

This mathematical lipid correction overestimated the $\delta^{13}C$ lipid correction for blue crab tissue from Mobile Bay (Vedral 2012); therefore, a mathematical lipid correction specific to crustacean tissues with C:N >4.5 (Bodin et al. 2007) was initially applied to crab, shrimp and stomatopod prey samples with elevated C:N ratios, which resulted in minor changes in $\delta^{13}C$ (mean ± SD $\delta^{13}C$ change = 0.58 ± 0.38‰, n = 93). Such a small change is likely not biologically relevant given the $\delta^{13}C$ range of these taxa groups. Also, invertebrate samples with high stores of chitin or glycogen can have C:N ratios similar to those in lipid-rich fish tissues, and lipid extraction does not result in a change in C:N ratios or $\delta^{13}C$ (Kiljunen et al. 2006, Logan et al. 2008). Hence, we present the measured $\delta^{13}C$ of all crustacean prey samples without lipid correction.

Contributions of prey items to red snapper diet were determined for each sampling year with a stable isotope mixing model in R ('simmr' package version 0.4.1, Parnell 2019). To avoid invalid extrapolations based on small sample sizes, prey items with n < 5 per year were not included in the mixing model inputs, which eliminated prey items identified as Nematoda, Salpidae, Thecosomata and several families of crabs, shrimp and fish. Trophic enrichment factors (TEFs) for $\delta^{13}C$ and $\delta^{15}N$ were set at 1 and 3‰,

respectively, with a standard deviation of 0.5 for each TEF (Rooker et al. 2006, Wells et al. 2008). Models were run 10 000 times, and all prey proportions reported are at the 50% quantile.

The calculated trophic position (TP) of each consumer is:

$$TP = (\delta^{15}N_{Consumer} - \delta^{15}N_{POM}) / \Delta n + 1 \quad (2)$$

where $\delta^{15}N_{Consumer}$ is that of the red snapper or prey item, $\delta^{15}N_{POM}$ is the 2 yr average $\delta^{15}N$ of POM collected at all sites from April to October during 2016 and 2017 ($\delta^{15}N$ = 4.35; Kohler 2020), and Δn is the TEF (3‰).

2.4. Statistical analysis

Spatial trends were analyzed using Mantel tests to determine spatial autocorrelation of red snapper and prey isotope data. For statistical analysis, red snapper weight and total length (TL) classes were divided into 1 kg and 100 mm incremental groupings while age was split into yearly cohorts. Variation in stable isotope values of red snapper between weight, TL and age classes, depth strata and structure type were assessed using a Kruskal-Wallis 1-way ANOVA in R with pairwise comparisons using Dunn's test of multiple comparisons using rank sums and Benjamini-Hochberg p-value adjustment to limit Type I errors. Variation in prey stable isotope values across depth strata and structure type were also analyzed using these tests by examining broad groupings of most prey types (shrimp, crabs, fish) due to low sample numbers of individual families. Nonparametric tests were run due to non-normality and inequality of variance of isotope data across the various groupings.

3. RESULTS

Over the 2 yr study period, 862 red snapper were examined: 456 in 2016 and 406 in 2017 (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m699p117_supp.pdf). More fish were collected from platforms (59.6%) than artificial reefs (40.1%), while only 2 fish (0.2%) were collected from bare-bottom control sites. Ages and TL ranged from 0.3 to 22 yr (median = 2.8 yr, mean ± SD = 3.0 ± 1.8 yr) and from 180 to 858 mm (median = 392 mm, mean = 412 ± 106 mm). Males and females were equally represented over the cumulative 2 yr period.

3.1. Red snapper SCA

Prey items were found in 76% of the examined red snapper. While some prey items could be identified to species, the resolution of the DNA barcoding was typically at the class or family level, so prey were grouped at these taxonomic levels with the exception of gastropods, which were identifiable to suborder Thecosomata. Unidentified crustaceans (2016: %W = 7.3, %FO = 61; 2017: %W = 2.5, %FO = 44) and teleosts (2016: %W = 11.8, %FO = 38; 2017: %W = 9.7, %FO = 45) were frequent for both years, as many samples were too small or degraded for genetic barcoding. The most frequently identified taxa in both years were stomatopods followed by portunid crabs (Table 1). %W values of prey were similarly ranked, with stomatopods having the largest value and Lutjanidae being the second ranked in 2016 and portunid crabs being second in 2017. In 2016, portunid crabs ranked third in %W while Sciaenidae ranked third in 2017. Crab prey consisted of 11 families in 2017 and 8 families in 2017, while shrimp prey included 5 families in 2016 and 8 families in 2017 (Table 1), with Mysidae, Penaeidae (brown and white shrimp), Penaeoidea (prawns) and Sergestidae ('krill-like' shrimps, all identified as *Acetes americanus*) all well represented in one or both years. Fish prey items had the highest taxonomic diversity among any of the broad prey categories, with 17 families identified in 2016 and 14 families in 2017, with Lutjanidae and Ophichthidae being the most frequently observed fish taxa in 2016 and 2017, respectively. Lutjanid prey items were all identified as red snapper.

3.2. Red snapper stable isotopes

The majority of red snapper isotope values fell within narrow ranges relative to prey items (Fig. 2). The average red snapper $\delta^{13}C$ in 2016 and 2017 were (mean ± SD) −16.7 ± 0.4 and −17.5 ± 1.2‰, respectively, with the difference being due to some individuals in 2017 having lower $\delta^{13}C$. No congruent differences were observed for $\delta^{15}N$ values for these individuals, and the average red snapper $\delta^{15}N$ values in 2016 and 2017 were not different (14.3 ± 0.4 and 14.2 ± 0.6‰, respectively). Most of the ^{13}C-depleted fish from 2017 were in narrow size and age ranges (250–500 mm TL; age 2–3 yr; Fig. 3). Mean isotopic values were similar between sexes (Table S1). Sampling location was not autocorrelated with red snapper $\delta^{13}C$ (Mantel R = 0.00421, $p < 0.0001$) but was with $\delta^{15}N$ (Mantel R = 0.169, $p < 0.0001$). Red snapper tissue $\delta^{13}C$

Table 1. Red snapper stomach content analysis frequency of occurrence (FO, n), %FO, weight (W, g) and %W by year for prey items that were collected more than once in 2016 or 2017

Prey type	Prey group	2016				2017			
		FO	%FO	W	%W	FO	%FO	W	%W
Nematode	Nematoda	0	0.00	0.00	0.00	2	0.60	0.02	0.00
Pyrosome	Pyrosomatidae	0	0.00	0.00	0.00	3	0.90	47.19	3.18
Salp	Salpidae	9	2.59	0.61	0.04	1	0.30	0.05	0.00
Bivalve	Mollusca	6	1.72	0.56	0.04	9	2.71	1.99	0.13
Bivalve	Bivalvia	17	4.89	1.39	0.09	1	0.30	0.03	0.00
Gastropod	Gastropoda	3	0.86	0.04	0.00	7	2.11	0.32	0.02
	Naticidae	0	0.00	0.00	0.00	2	0.60	6.96	0.47
	Pteropoda	11	3.16	6.26	0.42	37	11.14	17.13	1.16
Cephalopod	Cephalopoda	6	1.72	13.68	0.92	11	3.31	58.01	3.91
Ostracod	Ostracoda	5	1.44	0.11	0.01	1	0.30	0.02	0.00
Copepod	Caligidae	2	0.57	0.01	0.00	0	0.00	0.00	0.00
Amphipod	Amphipoda	23	6.61	1.66	0.11	16	4.82	0.90	0.06
Crab	Albuneidae	4	1.15	3.23	0.22	5	1.51	9.25	0.62
	Calappidae	28	8.05	4.78	0.32	1	0.30	0.40	0.03
	Hippoidea	2	0.57	7.50	0.51	0	0.00	0.00	0.00
	Paguroidea	4	1.15	0.23	0.02	0	0.00	0.00	0.00
	Parthenopidae	5	1.44	5.86	0.40	2	0.60	2.58	0.17
	Portunidae	53	15.23	179.38	12.12	61	18.37	164.92	11.12
	Pseudorhombilidae	9	2.59	13.12	0.89	2	0.60	3.16	0.21
	Raninidae	2	0.57	0.15	0.01	0	0.00	0.00	0.00
Shrimp	Alpheidae	2	0.57	0.89	0.06	2	0.60	0.13	0.01
	Mysidae	5	1.44	0.02	0.00	20	6.02	3.50	0.24
	Palaemonidae	0	0.00	0.00	0.00	4	1.20	0.11	0.01
	Penaeidae	14	4.02	83.78	5.66	12	3.61	41.85	2.82
	Penaeoidea	3	0.86	15.89	1.07	10	3.01	24.74	1.67
	Processidae	0	0.00	0.00	0.00	2	0.60	0.09	0.01
	Solenoceridae	0	0.00	0.00	0.00	6	1.81	2.01	0.14
	Sergestidae	0	0.00	0.00	0.00	12	3.61	78.98	5.33
Prawn	Luciferidae	0	0.00	0.00	0.00	2	0.60	0.01	0.00
Stomatopod	Stomatopoda	99	28.45	323.84	21.88	89	26.81	183.95	12.41
Fish	Bregmacerotidae	2	0.57	1.27	0.09	0	0.00	0.00	0.00
	Clupeidae	4	1.15	140.85	9.52	4	1.20	132.97	8.97
	Cynoglossidae	1	0.29	0.67	0.05	4	1.20	13.50	0.91
	Moringuidae	1	0.29	1.34	0.09	2	0.60	21.46	1.45
	Ophichthidae	3	0.86	16.31	1.10	11	3.31	84.71	5.71
	Ophidiidae	2	0.57	7.32	0.49	2	0.60	11.25	0.76
	Carangidae	2	0.57	3.75	0.25	2	0.60	0.11	0.01
	Lutjanidae	15	4.31	188.88	12.76	5	1.51	76.63	5.17
	Sciaenidae	4	1.15	119.74	8.09	5	1.51	137.23	9.25
	Triglidae	5	1.44	12.07	0.82	3	0.90	10.40	0.70

in 2016 significantly varied by TL, weight, age class and depth strata but not by structure type (Table 2). Pairwise comparisons using Dunn's test indicated that $\delta^{13}C$ of 2016 red snapper <300 mm were not different from 300–400 and 400–500 mm groups, but other groupings (400–500, 500–600 and >600 mm) were all different from each other ($p < 0.01$). Pairwise comparisons showed that the $\delta^{13}C$ of the following weight groups were not different: <0.5 vs. 0.5–1.0; 1.0–1.5 vs. 1.5–2.0; 1.5–2.0 vs. 2.0–2.5 and 2.5–3; 2.0–2.5 vs. 2.5–3.0 and >3.0; and 2.5–3.0 vs. >3.0 kg while all other groups were different from each other ($p < 0.039$). $\delta^{15}N$ significantly varied across of all of these parameter groupings. Pairwise comparisons indicated that the 2016 TL <300 mm group $\delta^{15}N$ was different from the 300–400 mm group ($p = 0.046$), the 400–500 mm group ($p = 0.008$) and the >600 mm group, which was also significantly different from all other groups ($p <$

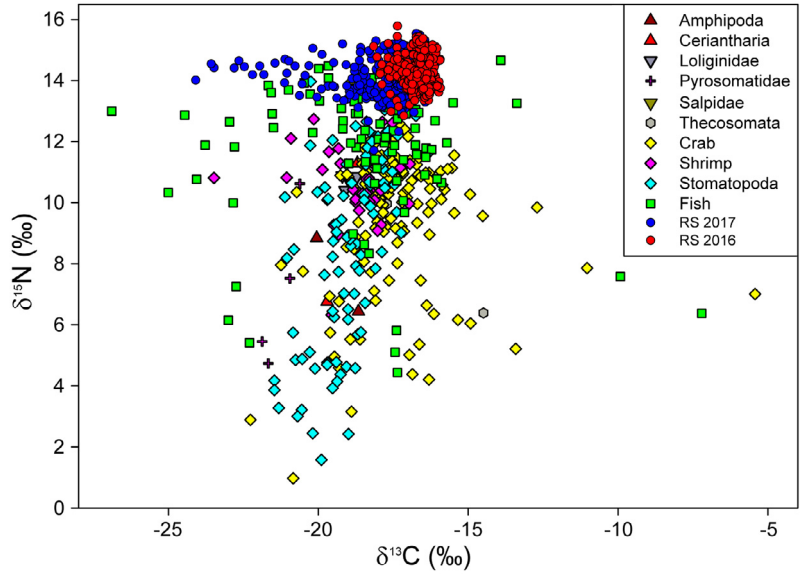

Fig. 2. Biplot ($\delta^{13}C$ vs. $\delta^{15}N$) of broadly grouped prey items along with red snapper (RS) collected in 2016 and 2017

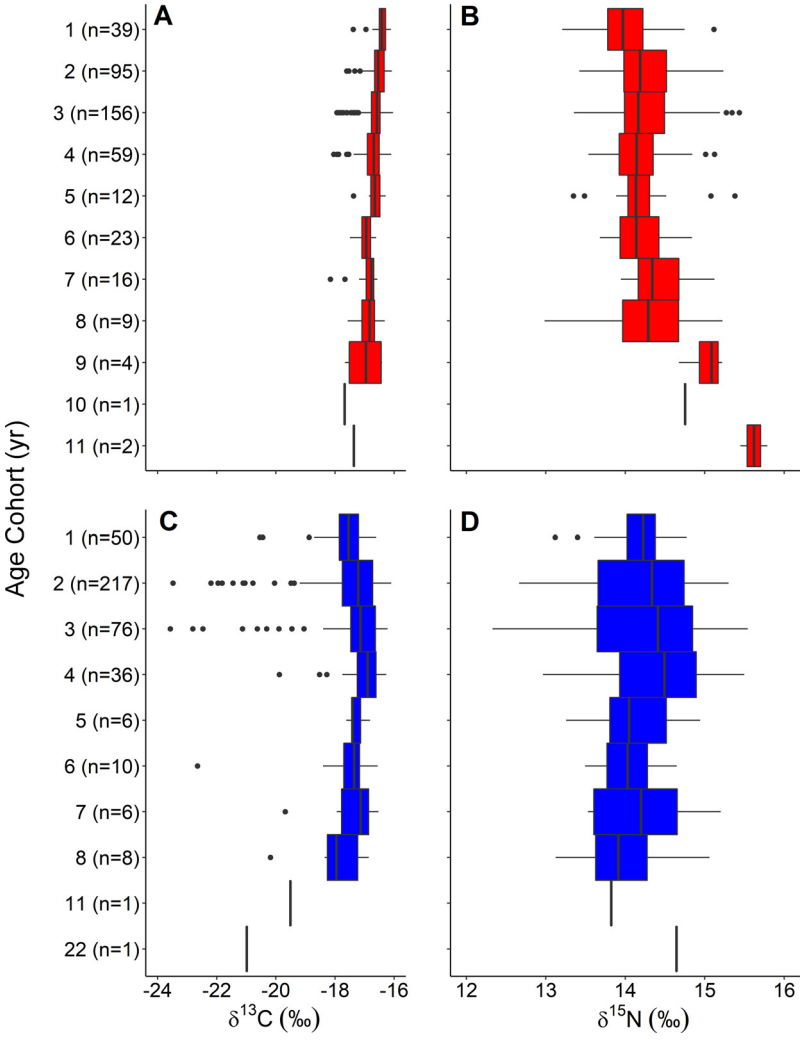

Fig. 3. Red snapper isotope values by age cohorts. (A) 2016 $\delta^{13}C$. (B) 2016 $\delta^{15}N$. (C) 2017 $\delta^{13}C$. (D) 2017 $\delta^{15}N$. Sample numbers are denoted for each age cohort in parentheses. The lines within boxes represent mean values and the boxes demarcate the 1st (25%) and 3rd (75%) quantiles. Whiskers represent minimum and maximum values, and outliers are shown as individual points

0.003). The 300–400 mm group did not vary significantly from the 400–500 mm group. The 500–600 mm group was not different from the <300, 300–400 or 400–500 mm groups. Pairwise comparison of weight groups showed that the <0.5 kg group was different from the 1.0–1.5 ($p = 0.005$), 1.5–2.0 (0.007) and >3.0 kg ($p < 0.001$) groups, and the latter was different from all other weight groups ($p < 0.032$). Pairwise comparisons of age groups showed that the age 2 group was different from the age 6 group ($p = 0.031$), but all other groups were not different. Mean $\delta^{13}C$ did not vary between structure types, but values significantly differed among depth strata ($p < 0.001$). Pairwise comparisons indicated that the shallow and mid strata were not different, but that the deep stratum differed from the shallow ($p < 0.001$) and mid ($p < 0.001$) strata.

In 2017, $\delta^{13}C$ significantly varied among groups based on TL ($\chi^2 = 15.639$, df = 4, $p < 0.001$), weight groups ($\chi^2 = 17.38$, df = 6, $p < 0.001$) and structure type ($\chi^2 = 29.738$, df = 1, $p < 0.001$) but not between age groups or depth strata (Table 3). Pairwise comparisons showed that $\delta^{13}C$ for the <300 mm TL group was different from the 300–400 ($p = 0.019$), 400–500 (0.021) and 500–600 mm ($p = 0.015$) groups and the >600 mm group was different from the 300–400 ($p = 0.031$), 400–500 ($p = 0.012$) and 500–600 mm ($p = 0.021$) groups, while all other groups were not different. Among weight groups, pairwise comparisons indicated that the <0.5 kg group was different from the 0.5–1.0 ($p = 0.039$) and the 2.0–2.5 kg ($p = 0.038$) groups

Table 2. Results of Kruskal-Wallis tests for significant differences in red snapper length, weight and age groups in 2016. Dunn's test results shown for significant differences below the respective Kruskal-Wallis tests

	$\delta^{13}C$									$\delta^{15}N$								
Length class (mm)	χ^2	df	p							χ^2	df	p						
	60.72	4	<0.001							34.749	4	<0.001						
		<300	**300–400**	**400–500**	**500–600**						**<300**	**300–400**	**400–500**	**500–600**				
	300–400	0.416								**300–400**	0.046							
	400–500	0.120	0.010							**400–500**	0.008	0.081						
	500–600	<0.001	<0.001	<0.001						**500–600**	0.053	0.392	0.187					
	>600	<0.001	<0.001	<0.001	0.046					**>600**	<0.001	<0.001	<0.001	<0.001				
Weight class (kg)	χ^2	df	p							χ^2	df	p						
	72.476	6	<0.001							44.047	6	<0.001						
		<0.5	**0.5–1**	**1–1.5**	**1.5–2**	**2–2.5**	**2.5–3**				**<0.5**	**0.5–1**	**1–1.5**	**1.5–2**	**2–2.5**	**2.5-3**		
	0.5–1	0.470								**0.5–1**	0.075							
	1–1.5	0.039	0.018							**1–1.5**	0.001	0.013						
	1.5–2	<0.001	<0.001	0.056						**1.5–2**	0.007	0.091	0.362					
	2–2.5	<0.001	<0.001	0.003	0.132					**2–2.5**	0.027	0.219	0.304	0.402				
	2.5–3	<0.001	<0.001	0.007	0.086	0.313				**2.5–3**	0.212	0.424	0.223	0.291	0.366			
	>3	<0.001	<0.001	<0.001	0.013	0.141	0.386			**>3**	<0.001	<0.001	0.002	0.002	0.002	0.003		
Age class (yr)	χ^2	df	p							χ^2	df	p						
	46.64	8	<0.001							20.401	8	0.0089						
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
	2	0.44								**2**	0.458							
	3	0.112	0.032							**3**	0.200	0.101						
	4	0.048	0.011	0.208						**4**	0.240	0.145	0.412					
	5	0.039	0.031	0.122	0.253					**5**	0.137	0.142	0.237	0.226				
	6	<0.001	<0.001	<0.001	0.008	0.117				**6**	0.136	0.031	0.124	0.179	0.366			
	7	0.009	0.005	0.033	0.088	0.303	0.270			**7**	0.144	0.163	0.243	0.232	0.498	0.357		
	8	0.009	0.007	0.031	0.063	0.195	0.491	0.317		**8**	0.153	0.134	0.233	0.212	0.432	0.484	0.420	
	9	0.070	0.067	0.108	0.128	0.198	0.315	0.257	0.320	**9**	0.116	0.223	0.148	0.148	0.193	0.222	0.183	0.220
Structure Type	χ^2	df	p							χ^2	df	p						
	0.67552	1	0.4111							64.097	1	<0.001						
Depth Strata	χ^2	df	p							χ^2	df	p						
	27.078	2	<0.0001							31.056	2	<0.001						
	Dunn's	**Deep**	**Mid**							**Dunn's**	**Deep**	**Mid**						
	Mid	<0.001								**Mid**	<0.001							
	Shallow	<0.001	0.0551							**Shallow**	0.212	<0.001						

Table 3. Results of Kruskal-Wallis tests for significant differences in red snapper length, weight and age groups in 2017. Dunn's test results shown for significant differences below the respective Kruskal-Wallis tests

	$\delta^{13}C$						$\delta^{15}N$					
Length class (mm)	χ^2	df	p				χ^2	df	p			
	15.639	4.000	0.004				9.440	4.000	0.051			
	<300	**300–400**	**400–500**	**500–600**			**<300**	**300–400**	**400–500**	**500–600**		
300–400	0.019						0.391					
400–500	0.021	0.425					0.132	0.119				
500–600	0.015	0.132	0.166				0.047	0.047	0.158			
>600	0.269	0.013	0.012	0.012			0.382	0.390	0.361	0.141		
Weight class (kg)	χ^2	df	p				χ^2	df	p			
	17.380	6.000	0.008				19.149	6.000	0.004			
	<0.5	**0.5–1**	**1–1.5**	**1.5–2**	**2–2.5**	**2.5–3**	**<0.5**	**0.5–1**	**1–1.5**	**1.5–2**	**2–2.5**	**2.5–3**
0.5–1	0.039						0.238					
1–1.5	0.117	0.467					0.072	0.236				
1.5–2	0.310	0.240	0.260				0.336	0.494	0.277			
2–2.5	0.038	0.170	0.176	0.109			0.001	0.002	0.027	0.009		
2.5–3	0.125	0.269	0.254	0.171	0.486		0.225	0.255	0.344	0.253	0.257	
>3	0.173	0.033	0.039	0.152	0.039	0.060	0.269	0.329	0.397	0.349	0.024	0.346
Age class (yr)	χ^2	df	p				χ^2	df	p			
	10.397	8.000	0.238				13.502	8.000	0.096			
Structure type	χ^2	df	p				χ^2	df	p			
	29.738	1.000	<0.001				87.101	1	<0.001			
Depth strata	χ^2	df	p				χ^2	df	p			
	5.096	2.000	0.078				43.010	2.000	<0.001			
	Dunn's	**Deep**	**Mid**				**Dunn's**	**Deep**	**Mid**			
	Mid	0.080					**Mid**	<0.001				
	Shallow	0.271	0.063				**Shallow**	0.140	<0.001			

while the >3.0 kg group was different from the 0.5–1.0 (p = 0.033), 1.0–1.5 (p = 0.039) and 2.0–2.5 kg (0.039) groups. All other weight groups were not different from each other. In 2017, $\delta^{15}N$ significantly varied across groups based on weight (p = 0.004), structure type (p < 0.001) and depth strata (p < 0.001) but not with TL or age. Pairwise comparisons of the weight groups indicated that the 2.0–2.5 kg group was significantly different than the <0.5 (p < 0.001), 0.5–1.0 (p = 0.002), 1.0–1.5 (0.027) and 1.5–2.0 kg (p = 0.009) groups, while the remaining weight groups were not different from each other. For depth strata, Dunn's pairwise comparisons indicated that mid stratum $\delta^{15}N$ values were different from shallow (p < 0.001) and deep strata (p < 0.001), but shallow and deep $\delta^{15}N$ were not different from each other.

3.3. Stable isotope values of prey items

Prey items occupied a broad range of isotope values relative to red snapper samples (Fig. 2). The crab families Portunidae (swimming crabs, namely *Callinectes similis*, *Ovalipes floridanus*, *Portunus gibbesii* and *P. sayi*) and Pseudorhombilidae (mud crabs, all *Speocarcinus lobatus*) were the most represented crabs obtained for SIA (Fig. 4). Less represented crab prey groups included the superfamilies Aethroidea (calico crabs) and Hippoidea (sand crabs), and families Albunidae (mole crabs), Menippidae (stone crabs) and Parthenopidae (elbow crabs). The average $\delta^{13}C$ for Portunidae did not vary across depth strata (Table S3). The $\delta^{15}N$ of crab prey was variable within families, and Portunidae had the highest $\delta^{15}N$ variability. Location was not autocorrelated to crab prey isotope values ($\delta^{13}C$ Mantel R = 0.02084, p = 0.22328; $\delta^{15}N$ Mantel R = 0.04734, p = 0.05794). Crab $\delta^{13}C$ values did not significantly vary with depth strata in 2016 but did in 2017 (p = 0.045) (Table 4). Dunn's pairwise comparisons indicated that the shallow stratum was different from the mid stratum (p = 0.019), but there was no difference between the shallow and deep strata or the mid and deep strata. Crab $\delta^{13}C$ did not vary by structure type in 2016 but did in

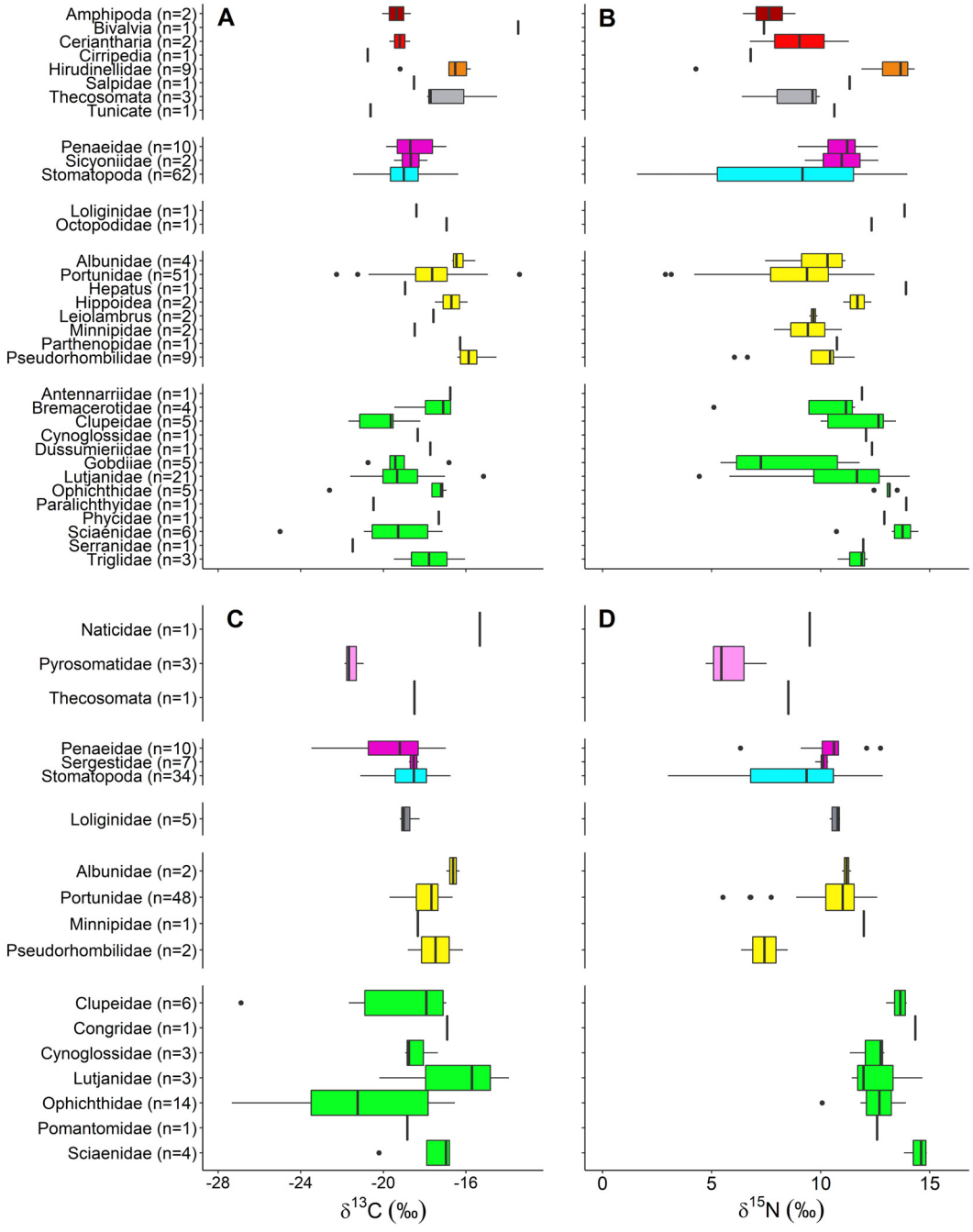

Fig. 4. Red snapper stomach content taxonomic group stable isotope values by sampling year. (A) 2016 $\delta^{13}C$. (B) 2016 $\delta^{15}N$. (C) 2017 $\delta^{13}C$. (D) 2017 $\delta^{15}N$. Sample numbers are denoted for each taxonomic group in parentheses. Box plot parameters as in Fig. 3

2017 ($p = 0.005$) (Table 5). Crab $\delta^{15}N$ values were not different by structure type in 2016 or 2017 or across depth strata in 2016 but there were differences in depth strata in 2017 ($p = 0.03$), and Dunn's pairwise comparisons indicated no difference between shallow and mid strata groups, but the deep stratum group was different from the shallow ($p = 0.045$) and mid strata ($p = 0.020$) groups.

The $\delta^{13}C$ of shrimp prey groups ranged from −23.5 to −16.9 ‰ across the 2 sampling years, while $\delta^{15}N$ fell in a relatively narrow range (Fig. 4). Most of the shrimp prey available for SIA (65%) were from fish caught in the mid depth stratum. Penaeid shrimp from the shallow depth stratum in 2017 had higher $\delta^{13}C$ variability compared to those from 2016 and other strata, and the highest $\delta^{13}C$ values were from

Table 4. Prey isotope Kruskal-Wallis tests comparing prey stable isotope values by structure type and depth strata. Dunn's test results shown for significant differences found with Kruskal-Wallis tests

		$\delta^{13}C$			$\delta^{15}N$		
		χ^2	df	p	χ^2	df	p
2016							
Fish	Structure type	0.1327	1	0.7157	1.4015	1	0.2365
	Depth strata	1.9112	2	0.3846	6.1451	2	**0.0463**
					Dunn's	**Deep**	**Mid**
					Mid	0	
					Shallow	0	0.4040
Crab	Structure type	1.6718	1	0.1960	0.0326	1	0.8568
	Depth strata	0.3047	2	0.8579	1.5568	2	0.4591
Mantis Shrimp	Structure type	0.4827	1	0.4872	0.0071	1	0.9331
	Depth strata	8.8056	2	**0.0122**	6.9557	2	**0.0309**
		Dunn's	**Deep**	**Mid**	**Dunn's**	**Deep**	**Mid**
		Mid	0.0111		**Mid**	0.0137	
		Shallow	0.0113	0.1047	**Shallow**	0.0764	0.4839
Shrimp	Structure type	5.3333	1	**0.0209**	4.6875	1	**0.0304**
	Depth strata	3.4167	2	0.1812	0.0292	2	0.9855
					Dunn's	**Deep**	**Mid**
					Mid	0.4929	
					Shallow	0.6954	1.0000
		χ^2	df	p	χ^2	df	p
2017							
Fish	Structure type	8.9792	1	**0.0027**	0.0000	1	1.0000
	Depth strata	2.5934	2	0.2734	0.3122	2	0.8555
Crab	Structure type	7.8186	1	**0.0052**	6.9951	2	**0.0303**
	Depth strata	6.1954	2	**0.0452**	6.9951	2	**0.0303**
		Dunn's	**Deep**	**Mid**	**Dunn's**	**Deep**	**Mid**
		Mid	0.4204		**Mid**	0.0200	
		Shallow	0.3270	**0.0194***	**Shallow**	0.0447	0.0540
Mantis Shrimp	Structure type	3.7735	1	0.0521	12.4160	1	**0.0004**
	Depth strata	4.7360	2	0.0937	9.6111	2	**0.0082**
					Dunn's	**Deep**	**Mid**
					Mid	0.0058	
					Shallow	0.0592	0.0429
Shrimp	Structure type	0.7948	1	0.6721	3.1791	1	0.2040
	Depth strata	0.7778	2	0.6778	0.1307	2	0.9367

the shallow and deep strata in 2016 (Table S3). Shrimp prey $\delta^{13}C$ was spatially autocorrelated (Mantel R = 0.04558, p = 0.025597), but $\delta^{15}N$ was not (Mantel R = 0.1935, p = 0.08). Shrimp $\delta^{13}C$ was not different by depth strata in either year (Table 5), but there were $\delta^{13}C$ differences between structure type in 2016 (p = 0.021) but not in 2017.

Stomatopod samples had a lower $\delta^{13}C$ range (–21.5 to –16.4‰) than crabs and shrimp but had the broadest $\delta^{15}N$ range (1.6 to 14.0‰) of any prey group. Stomatopod $\delta^{13}C$ values were not different between structure type groups in either year (Table 5), and $\delta^{15}N$ did not differ by structure type groups in 2016 but did vary between structure types in 2017 (p = 0.00426). Stomatopod $\delta^{13}C$ values were different between depth strata in 2016 (p = 0.031) (Table 5) but not in 2017. Dunn's pairwise comparison indicated that $\delta^{13}C$ from the shallow and mid strata in 2016 were not different, but both shallow and mid strata were different from the deep stratum. Stomatopod $\delta^{15}N$ values were different between depth strata in both years (Table 5). Pairwise comparisons for 2016 indicated no difference between the shallow and mid or shallow and deep groups, but the mid stratum group was different from the deep group, while in 2017 the shallow stratum was different from the mid stratum, which was different from the deep stratum, but there was no difference between the shallow and deep strata. In 2016, stomatopod $\delta^{13}C$ and $\delta^{15}N$ isotopes were significantly autocorrelated ($\delta^{13}C$: Mantel

R = 0.14, p = 0.0013; $\delta^{15}N$: Mantel R = 0.101, p = 0.0055), but not in 2017 ($\delta^{13}C$: Mantel R = 0.0213, p = 0.3605; $\delta^{15}N$: Mantel R = 0.074, p = 0.171). Stomatopod larvae generally had lower mean $\delta^{15}N$ (5.4 ± 2.8‰ SD, n = 13) than other stomatopod samples (9.4 ± 2.8‰, n = 82).

The fish prey had the largest range in $\delta^{13}C$ any prey group (–25.1 to –7.1‰; Figs. 2 & 4). Low sample numbers prevented comparisons of isotope values of most fish families across years and depth strata (Fig. 4A); however, the $\delta^{13}C$ of fish prey as a group did not vary significantly between structure type or depth strata in 2016 (Table 5). In 2017, fish prey $\delta^{13}C$ significantly varied between artificial reefs and platforms (p = 0.003) but not between depth strata (Table 5). Fish prey $\delta^{15}N$ in both years ranged from 5.1 to 14.9‰ (Fig. 4). Lutjanidae prey items had a broad range of $\delta^{15}N$ with a lower mean (11.0 ± 2.4‰) than the captured red snapper (Tables S1, S2 & S4). Shallow stratum Ophichthidae in 2017 were more enriched on average in $\delta^{15}N$ than the mid or deep strata samples, which were similar to each other (Table S4). Nitrogen stable isotope values did not significantly vary between structure type in 2016 or 2017, and $\delta^{15}N$ was different between depth strata (p = 0.046) in 2016 but not in 2017. Pairwise comparisons of 2016 fish $\delta^{15}N$ by depth strata indicated that the shallow and mid strata values were not significantly different from each other but that the deep stratum was significantly different from the shallow (p = 0.033) and mid strata groups (p = 0.039). Neither $\delta^{13}C$ nor $\delta^{15}N$ was spatially autocorrelated ($\delta^{13}C$ Mantel R = 0.03869, p = 0.13179; $\delta^{15}N$ Mantel R = –0.0003187, p = 5.0085).

3.4. Isotope mixing model

Since there were no consistent isotopic differences among red snapper sexes, age and size classes, habitat types or depth strata, mixing models were applied to all red snapper for each sampling year. Mixing model 'simmr' results for 2016 indicated that Sciaenidae fishes made up 38.7% of the red snapper diet, followed by Penaeidae shrimp (17.7%), stomatopods (13.1%), Lutjanidae fishes (10.3%), Portunidae crabs (9.2%), and Pseudorhombilidae crabs (6.7%) (Fig. 5A). In 2017, the largest dietary proportion was Portunidae crabs (55.6%) followed by Clupeidae (17.2%) and Ophichthidae fishes (10.9%), Sergestidae (5.2%), Penaeidae (4.4%) and Stomatopods (4.2%) (Fig. 5B).

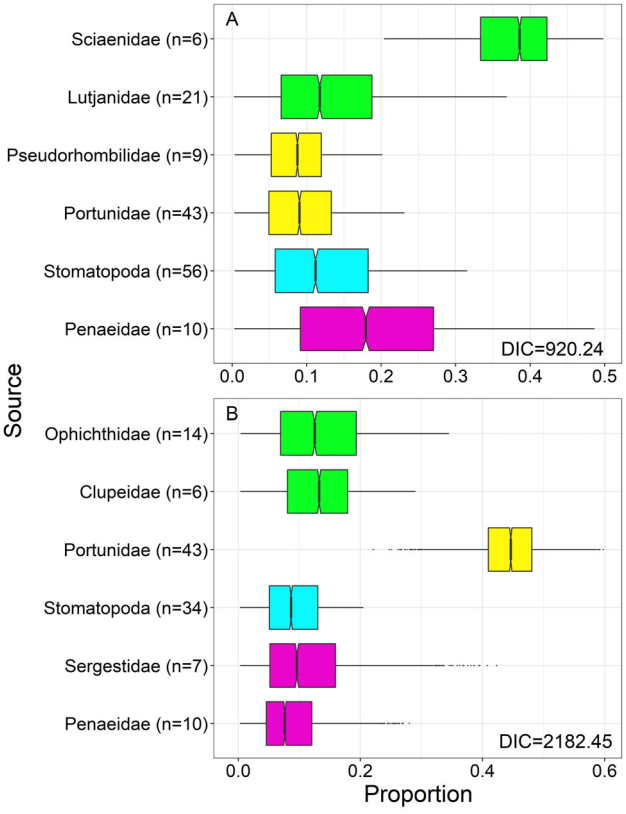

Fig. 5. Stable isotope mixing model dietary proportions from the 'simmr' mixing model for red snapper collected in (A) 2016 and (B) 2017. Sample numbers are denoted for each taxonomic group in parentheses. Box plot parameters as in Fig. 3. DIC: deviance information criterion

3.5. TP estimates

The estimated predatory red snapper TP ranged from 3.4 to 4.8, with an average of 4.2 ± 0.1 (SD). Crabs had average TPs from 1.8 (Calappidae) to 4.2 (Aethridae; species *Hepatus epheliticus*, calico crab) (Table 5). The calculated TPs for Portunidae and Pseudorhombilidae were similar (2.8 ± 0.8 and 2.6 ± 0.7, respectively). Stomatopods had the largest calculated TP range with some unrealistically low estimates (>1) while others had TPs as high as 4.2, but the average TP estimate was 2.5 ± 1.0. Of the fish prey, Gobiidae had the lowest average TP (2.0 ± 0.8) and Sciaenidae the highest (4.1 ± 0.4) (Table 2).

4. DISCUSSION

4.1. Diet SCA

In both years, SCA indicated that red snapper diet contained a wide variety of prey groups, many in low

Table 5. Trophic position (TP) calculations (n, mean, min and max) for red snapper prey items compared with literature (lit) TP values of prey groups when available. Asterisks indicate values based on size and trophic levels of closest relatives. NA: not available

Prey type	Prey group	n	Mean TP	Mean SD	Min TP	Max TP	Lit TP	Reference(s)
Anemone	Ceriantharia	2	2.6	1.1	1.8	3.3	NA	
Tunicate	Tunicata	4	1.9	0.9	1.1	3.1	NA	
Salp	Salpidae	1	3.3				NA	
Gastropod	Sinum	1	2.7				NA	
	Thecosomata	4	2.4	0.5	1.7	2.9	NA	
Cephalopod	Loliginidae	6	3.3	0.4	3.0	4.2	3.7 ± 0.4 SD	Coll et al. (2013)
Amphipod	Amphipoda	2	2.1	0.6	1.7	2.5	1.7–2.5	Vinagre et al. (2012)
Shrimp	Litopenaeus	6	3.1	0.4	2.6	3.8	NA	
	Penaeoidea	14	3.1	0.5	1.7	3.8	2.1	Akin & Winemiller (2008)
	Sergestidae	7	2.9	0.1	2.8	3.0	NA	
Prawn	Sicyoniidae	2	3.2	0.8	2.6	3.8	NA	
Crab	Aethridea	1	4.2				NA	
	Albunidae	6	3.0	0.5	2.0	3.3	NA	
	Calappidae megalope	4	1.8	0.4	1.2	2.1	NA	
	Hippoidea megalope	2	3.4	0.3	3.2	3.7	NA	
	Menippidae	3	3.0	0.7	2.2	3.5	NA	
	Parthenopidae	3	2.9	0.2	2.7	3.1	NA	
	Portunidae	99	2.8	0.8	0.5	3.7	3.0 to 3.3	Carozzo et al. (2014), Careddu et al. (2017)
	Pseudorhombilidae	11	2.6	0.7	1.6	3.4	NA	
Stomatopod	Stomatopoda	95	2.5	1.0	0.1	4.2	3.5	Antony et al. (2010)
Fish	Antennarriidae	1	3.5				3.5 ± 0.6 SE	FishBase*
	Bregmacerotidae	4	2.8	1.0	1.3	3.4	3.1 ± 0.3 SE	FishBase*
	Clupeidae	11	3.8	0.5	2.9	4.2	3.4 to 3.8	Motta et al. (1995), Vega-Cendejas et al. (1994)
	Cynoglossidae	1	3.6				3.3 ± 0.4 SE	FishBase*
	Dussumieriidae	2	3.9	0.4	3.7	4.2	3.6 ± 0.2 SE	FishBase (diet studies)
	Gobiidae	4	2.0	0.8	1.4	3.1	3.2 ± 0.3 SE	FishBase*
	Lutjanidae	19	3.2	0.8	1.5	4.2	NA	
	Ophichthidae	13	3.7	0.3	2.9	4.2	3.0	Akin & Winemiller (2008)
	Ophidiidae	2	4.0	0.1	3.9	4.1	NA	
	Phycidae	1	3.9				NA	
	Pomatomidae	1	3.7				NA	
	Sciaenidae	9	4.1	0.4	3.1	4.5	3.1 to 3.5	Akin & Winemiller (2008), Wilson et al. (2009)
	Serranidae	1	3.5				NA	
	Triglidae	2	3.4	0.3	3.1	3.6	3.5	FishBase*

numbers, but the most frequently identified prey were consistently stomatopods and portunid crabs. These results support red snapper being generalist predators that consume a wide array of prey types, presumably based on availability (Wilson & Nieland 2001, Szedlmayer & Lee 2004, Brewton et al. 2020). Consistent with our study, portunid crabs and stomatopods have been shown to be common prey for mature red snapper, making up a large proportion of their identified diet (Wells et al. 2008, Dance et al. 2018, Brewton et al. 2020). The limitation of sample size for genetic barcoding resulted in a high proportion of unidentified prey items which limited its usefulness in providing fine taxonomic resolution for all stomach contents; however, barcoding did provide useful information on specific taxa that would not have otherwise been identified.

4.2. Diet proportion results from 'simmr'

The 'simmr' model suggested that red snapper diet varied annually, with sciaenid fishes being the greatest contributor in 2016 and portunid crabs in 2017. In both years, the remaining proportions were split evenly across other prey taxa, which is a common result when mixing models cannot elucidate contributions of sources with high confidence, which makes it difficult to assess if these results are reflective of the true diet or an artifact of variable isotope values or a

combination of both. The low $\delta^{13}C$ values for some red snapper likely resulted in a higher proportion of isotopically lighter fish prey items (Ophichthidae and Clupeidae) in the 2017 'simmr' model. Ophichthidae were more prevalent 2017, and both of these fish groups had lower $\delta^{13}C$ values in 2017 than in 2016, likely resulting in this annual difference.

While SCA and 'simmr' results both agree with previous studies that red snapper have a diverse diet, the disconnect in results from the 2 analyses is likely due to several factors, the most obvious being the differences in prey items obtained for isotopic analysis between years. Many prey samples were too small or degraded for either analysis, and some samples had no remaining material after DNA barcoding, both of which are difficult issues to overcome with small, visually unidentifiable prey items. Independent sampling of the diverse prey types would enhance the viability of using stable isotope mixing models by better constraining prey isotope values and allowing assessment of prey size on stable isotope values which would better inform mixing model inputs. However, this would require a greater sampling effort with various gear types which was not feasible and was well outside the scope of this study. Several of the prey groups such as Stomatopoda and Portunidae had highly variable isotopic values that are likely size related and would lead to large uncertainties in the model outputs (Bond & Diamond 2011). This is particularly true of stomatopod $\delta^{15}N$ values, which spanned a range of >12‰ over both years.

4.3. TP estimates

Red snapper average $\delta^{15}N$, and hence TP estimates, across both years were nearly identical despite their highly varied diet. Our estimated average TP (4.2 ± 0.1 SD) is slightly higher than the previous estimates of 3.85 ± 0.13 SE (Tarnecki & Patterson 2015) and 3.90 ± 0.72 SE (FishBase 2022).

TP estimates for many of the prey groups were similar to those reported in the literature. Crabs as a broad group have high variability, but most of the individual families have smaller ranges. A few of the individual Portunidae, Pseudorhombilidae and Stomatopoda samples had $\delta^{15}N$ values that were less than the baseline $\delta^{15}N$ values used to estimate TP, suggesting that some basal resources were not isotopically characterized in this study. Benthic microalgae from sandy bottoms surrounding structure have been shown to contribute to red snapper diet (Wells et al. 2008), while macroalgae and epiphytes growing on hardened structures may also contribute to reef food webs (Daigle et al. 2013). Phytoplankton around and epiphytes attached to petroleum platforms have higher seasonal $\delta^{15}N$ variability (2.4–6.3 and 4.7–6.3‰, respectively) than attached red and green algae (2.3–3.4 and 3.9–4.2‰, respectively) and differences between some primary producers collected simultaneously were >4‰ (Daigle et al. 2013). It is also possible some POM samples used to characterize the mean $\delta^{15}N$ baseline included microzooplankton. The isotope values and C:N ratios of POM in the region are highly variable (Kohler 2020), suggesting a dynamic plankton population driven by highly fluctuating freshwater inputs to the region (Slife 2022). Despite this variability in primary producers and POM, the mean base $\delta^{15}N$ used herein is similar to those of other studies from the northern GOM (Rooker et al. 2006, Simonsen et al. 2015, Dance et al. 2018).

The stomatopod $\delta^{15}N$ range suggests they feed across 3 trophic levels in the study region, and some feed at trophic levels which rival or exceed those of some fish prey. Similarly, high TPs were seen for some crabs, which may be due to scavenging or direct consumption of small fish and other crabs. For blue crabs, cannibalism increases with size and can account for up to 15–25% of the adult diet (Li et al. 2011). While most fish prey TP ranges were similar to those reported for fish in the literature, 2 benthopelagic families (Bregmacerotidae and Gobiidae) were represented by some individuals that also had lower $\delta^{15}N$ than POM, resulting in unrealistically low TP estimates, which supports the idea that some organisms are utilizing a benthic basal resource with lower $\delta^{15}N$. Some Lutjanidae prey also had low $\delta^{15}N$ and resultant TP, which could be attributed to the use of isotopically lighter basal resources or could indicate that these fish were recent reef arrivals that had migrated from a region with lower base $\delta^{15}N$ values.

4.4. Isotopic variability and impacts on the 'simmr' model

Similar to many previous studies in the northern GOM, most red snapper samples showed little isotopic variability (Wells et al. 2008, Simonsen et al. 2015, Brewton et al. 2020). While some statistical isotopic differences were found among size and age classes as well as by habitat type and depth strata in each sampling year, we found no consistent differences between the 2 years of the study. The lower $\delta^{13}C$ values for some age 2–3 fish may be indicative of individuals recently migrating from more inshore

waters where more ^{13}C-depleted basal resources (terrestrial C3, *Juncus romarianus*, benthic microalgae, phytoplankton) are more prevalent (Dillon et al. 2015). This generally agrees with when mature red snapper migrate to various types of high relief structure between ages 1 and 2 yr (Gallaway et al. 2009, Cowan et al. 2011) considering fish muscle turnover rates which can range from weeks to months (Buchheister and Latour 2010, Nelson et al. 2011).

Since 'simmr' models consider multiple isotopes, high isotopic variability of sources inherently leads to higher uncertainties in model results. The broad $\delta^{15}N$ (and resultant TP) ranges in the Portunidae, Pseudorhombilidae and Stomatapoda prey indicate that these organisms feed across multiple trophic levels likely due to size differences and/or may be utilizing prey that are dependent on primary producers with $\delta^{15}N$ values lower than POM, which is difficult to discern with bulk $\delta^{15}N$ alone. Prey size could not be evaluated in our study, but ontogenetic shifts in diet and stable isotope values are well described in crustaceans (Fry & Arnold 1982, Raz-Guzmán & Dela-Lanza 1993, Fry et al. 2003), and stomatopods are known to feed at progressively higher TP as they grow from planktonic larvae to aggressive benthic predators as adults (Caldwell & Dingle 1976).

Ophichthidae prey from 2017 in the shallow stratum had higher $\delta^{15}N$ than those from the other depth strata, which may indicate a spatial isotope baseline shift moving from nearshore to offshore, but *Lutjanus* prey items did not show the same pattern and had higher isotopic variability. The prey items genetically identified as lutjanids, specifically *L. campechanus*, were depleted in both ^{13}C and ^{15}N relative to the targeted red snapper, with calculated TPs approximately 1 trophic level lower. Cannibalism in fish is generally considered rare outside of aquaculture settings, although it has been documented in many wild fish populations, most commonly in piscivorous fishes (Pereira et al. 2017). It has long been speculated that cannibalism is a density-dependent regulator of populations (Ricker 1954), but this remains a controversial subject (Pereira et al. 2017). Some red snapper cannibalism occurs in aquaculture settings when no other prey is available (Bailey et al. 2001, Leu et al. 2003), but cannibalism was not observed in a coastal Alabama field study although adults did aggressively defend their habitat by chasing away smaller competitors (Piko & Szedlmayer 2007).

It is unclear how environmental parameters may affect red snapper foraging in this hydrologically dynamic region. Highly variable turbidity levels are common to the region (Hoover et al. 2022), and fish are more abundant in less turbid estuarine waters while crabs and shrimp were more abundant when turbidity was high (Lunt & Smee 2014). Increased turbidity reduces feeding efficiencies of some visual predators, leading to reduced growth rates (Snow et al. 2018) which could enhance the likelihood of red snapper cannibalism. It is also possible that there was misidentification by DNA barcoding at the species level, which can be problematic due to mistakes made in acquiring and analyzing genetic sequences that populate genetic data bases such as BOLD and GenBank (Meiklejohn et al. 2019, Pentinsaari et al. 2020). There are 13 other Lutjanidae species found in the Western Atlantic and northern GOM (Gold et al. 2011), so it is possible that other species may have been misidentified by DNA barcoding.

5. CONCLUSION

Our results help develop a better understanding of red snapper ecology and reef food webs in the northern GOM. The novel use of SCA prey items for SIA allowed many taxonomic groups to be collected and isotopically characterized, which can contribute to EBFM for the region. Consistent with previous studies that were more limited in time and space, red snapper in this study are generalist top predators that utilize a wide array of diverse prey items. Regional differences in red snapper diets across the northern GOM have been attributed to regional and temporal differences in prey fields, although the drivers of these differences are not well understood (McCawley et al. 2003, Tarnecki & Patterson 2015). While it is difficult to discern whether our SCA or 'simmr' results give the best estimate of 'true' diet, results from both show that the utilized prey field is taxonomically and isotopically diverse. The consistency of individual red snapper isotope values with an isotopically variable prey field suggests that these fish serve as stable isotope integrators of reef food webs, each feeding somewhat evenly across a taxonomic and isotopically variable prey field. While temporal and spatial heterogeneity in diet may be due to differences in the available prey, some may be due to the ability of red snapper to locate and capture prey in a dynamic water column where high turbidity and hypoxia are common (Brunner et al. 2006, Hoover et al. 2022). Future studies with independent prey sampling using multiple gear types and methods would better elucidate the structure of reef food webs in this hydrologically dynamic region. Such efforts should examine spatial and temporal distributions of prey

types, prey sizes and isotope values, which would improve our understanding of red snapper feeding ecology as well as the overall structure of northern GOM reef food webs.

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