FEEDING ECOLOGY OF GRAY TRIGGERFISH (*BALISTES CAPRISCUS*) AND RED SNAPPER (*LUTJANUS CAMPECHANUS*) AT ARTIFICIAL REEFS IN THE NORTHWEST GULF OF MEXICO

A Thesis

by

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ABSTRACT

This study examined the feeding ecology of two reef fishes using gut content and stable isotope analyses to assess the role of artificial reefs as foraging habitat in the Northwest Gulf of Mexico (GoM). Reefs were divided into three regions (north, central, south) across a north to south gradient of increasing salinity due to decreasing rates of freshwater inflow. Crabs were the dominant prey for both Gray Triggerfish *Balistes capriscus* (24 %), and Red Snapper *Lutjanus campechanus* (27 %). Gray Triggerfish consumed more xanthid crabs, pelagic gastropods, and reef associated prey, while non-reef prey (portunid crabs, fish, stomatopods) were prominent in Red Snapper. Natural stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were measured for primary producers and muscle tissue of both species, and examined by age, species, and region. Muscle tissue $\delta^{13}C$ and $\delta^{15}N$ values increased with ontogeny for each species. Gray Triggerfish had lower $\delta^{13}C$ and $\delta^{15}N$ values across all age classes and a larger Standard Ellipse Area (SEA_c) relative to Red Snapper. Contribution estimates of particulate organic matter (POM, 32 – 60 %) and benthic microalgae (BMA, 40 – 68 %) were comparable for each species, with greater BMA contributions within most age classes ($\bar{x}$ difference = 21.8 %). Red Snapper gut contents and stable isotope values of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ differed across regions. Red Snapper from the south region showed differing trends with ontogeny ($\delta^{15}N$ decreased with fish size), and a larger SEA_c compared to the north and central regions. This study demonstrates differences in feeding and resource partitioning between Gray Triggerfish and Red Snapper across multiple age classes, as well as the importance of benthic (BMA) primary production to consumers at artificial reefs in the GoM.

DEDICATION

For my parents, Vaylan and Katherine, whose life-long encouragement and support has made my professional and personal aspirations possible, and my husband, Michael, for his reassurance and love during this endeavor.

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All work, data collection, sample processing, and data analysis, for the thesis was completed by the student, under the advisement of Dr. R.J. David Wells of the Department of Marine Biology.

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INTRODUCTION

Artificial reefs are frequently deployed in marine ecosystems to increase fisheries yields and enhance production of reef-associated fauna (Baine 2001, Charbonnel et al. 2002, Sutton & Bushnell 2007). These goals are contingent on the premise that artificial reefs provide reef fishes and invertebrates with functionally similar habitat to natural reefs (Bohnsack & Sutherland 1985, Shipp & Bortone 2009). While it is evident that high densities of economically and ecologically important species are often associated with artificial reefs (Brickhill et al. 2005, Goldman et al. 2016), their ecological role has continually been debated (Grossman et al. 1997, Lindberg 1997) and remains unresolved (Burt et al. 2009, Macreadie et al. 2011, Koeck et al. 2014). Nevertheless, global use of artificial reefs as fisheries management tools continues to increase (Tessier et al. 2015, Becker et al. 2016), thus there is a need to determine the functional role artificial reefs provide to economically important species to promote effective conservation and management.

Determining the functional role of artificial reefs is a multidisciplinary aim, encompassing aspects of behavioral ecology, life history, and environmental factors. Studies investigating trophic interactions of faunal communities can provide useful data on sources of production and energy pathways (Daigle et al. 2013, Cresson et al. 2014, Frisch et al. 2014). Despite the use of these structures by many economically valuable fishes (Ajemian et al. 2015); our understanding of the feeding ecology for common predators (i.e., snappers, groupers) associated with artificial reefs remains limited (Tarnecki & Patterson 2015). Examination of predatory reef fishes diets and trophic interactions, and identification of sources of primary production, is needed at artificial reefs to better understand their role as habitat to these species.

Studies combining conventional gut content analysis and natural stable isotopes have been used to reconstruct feeding patterns and discern complex trophic interactions of faunal communities (France et al. 1995, Créach et al. 1997, Wells et al. 2008). Gut content analysis is an indicator of recent (hours to days) feeding habits (Bowen 1996), and can be used to discern detailed predator-prey interactions and indicate potential competition between or within species (Ahlbeck et al. 2012). Natural stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) provide a long-term measure of diet, track energy flow through trophic pathways, and determine trophic position (Peterson & Fry 1987, Post et al. 2002, Lajtha & Michener 2008). $\delta^{13}C$ and $\delta^{34}S$ values of predators reflect consumer diet and are useful for discerning contributions from different primary producers (e.g. pelagic vs. benthic), while nitrogen ($\delta^{15}N$) can be used to estimate trophic position (Post et al. 2002, Lajtha & Michener 2008). Even though stable isotopes are commonly used to discern complex trophic interactions, this technique alone lacks the resolution needed to reconstruct food webs and track energy flow (Post et al. 2002). Therefore, gut content analysis paired with stable isotopes results in a more integrative assessment of consumer feeding ecology than either method alone.

This study examined the feeding ecology of two reef fishes at artificial reefs in the Northwest Gulf of Mexico (GoM), Gray Triggerfish *Balistes capriscu*s and Red Snapper *Lutjanus campechanus*. These species are among the most abundant and frequently targeted fishes by recreational and commercial fisheries at artificial reefs in the GoM (Strelcheck et al. 2005, Addis et al. 2016). While Gray Triggerfish and Red Snapper often co-occur on artificial reefs and are dominant predators (Dance et al. 2011, Addis et al. 2013), our understanding of their interspecific trophic interactions is lacking. Current knowledge on Red Snapper feeding ecology is primarily limited to the Northeast and north-central GoM (Szedlmayer & Lee 2004, Wells et al. 2008, Zapp-Sluis et al. 2013, Simonsen et al. 2015), where biomass and fecundity

estimates are lower and physical and hydrographic conditions are considerably different from the Northwest GoM (Morey et al. 2003, Karnauskas et al. 2017). Information on the trophic ecology of Gray Triggerfish at artificial reefs in the GoM is even more limited (Frazer et al. 1991, Kurz 1995). The aim of this study was to use natural stable isotope analysis paired with gut content analysis to examine and contrast the role of artificial reefs as foraging habitat to these two reef predators. In addition, Red Snapper regional feeding patterns were examined across a north to south coastal gradient to examine spatial variation in diet.

MATERIALS AND METHODS

Study area and sample collection

Sampling occurred from May to August of 2015 at nearshore (< 60 km from the shoreline) artificial reefs in the Northwest GoM. Sites were distributed from north to south, and grouped into three regions [north (n = 2), central (n = 2), and south (n = 2)] (approximately 100 km apart, Figure A.1). Salinity is lowest and freshwater inflow is highest in the north region, and subsequent increases in salinity and decreases in the rate of freshwater input occur into the central and south regions (Tolan 2007). Reefs ranged from 13 to 32 m in depth, and were comprised of a variety of materials including quarry rocks, marad buoy pieces, concrete anchors and reef pyramids in the north region. The central region was comprised of quarry rocks, concrete blocks, culverts, reef balls, and disassembled platforms. In addition to structures present in the north and central regions (concrete blocks, culverts, pyramids, and disassembled platforms), the south region included ships.

Two sampling gears were used to obtain a wide size range of Gray Triggerfish and Red Snapper at each reef site, which were surveyed one to two times during the sampling period. Larger individuals were collected via standardized vertical longline surveys, using a protocol similar to the Southeast Area Monitoring and Assessment Program (SEAMAP) (Gregalis et al. 2012), while smaller individuals were targeted using trap surveys. Sampling at each artificial reef site consisted of three sets of vertical longline and paired trap deployments (total of six traps) at three locations. Each vertical longline set was comprised of four separate drops of a backbone (10 hooks), containing one of four hook sizes (2/0, 8/0, 11/0 and 15/0 circle hooks). Each hook size was fished for five minutes, while holding a fixed position over the reef. Oval fish traps (volume = 19,000 cm^3, mesh size = 0.63 cm) were soaked for approximately one hour.

Salinity, temperature, and dissolved oxygen were measured during each survey using a Hydrolab multiparameter sonde. In addition, particulate organic matter (POM) and benthic microalgae (BMA) were collected during surveys to measure stable isotope compositions of two primary sources (i.e., producers) of organic matter. Seawater was collected at each reef site, and POM was isolated by filtering seawater over precombusted (1 h at 450°C) 47 mm GF/F filters with a 0.7 μm pore size, and was used as a proxy for phytoplankton. Sediment was collected via a Ponar benthic grab (15.2 x 15.2 cm), from which BMA was isolated for stable isotope analysis following the vertical migration technique described by Wells et al. (2008).

Stable isotopes and gut content analysis

Fishes were immediately placed on ice in the field for transport back to the laboratory, where they were stored at -20°C until processing. Fishes were weighed to the nearest g and measured to the nearest mm straight total length (TL) and fork length (FL). The stomach and intestinal tract (gut) were removed from each individual, weighed to the nearest g, incised, fixed in 10 % formalin for 24 to 48 hours, and then preserved in 70 % ethanol until gut content analysis was performed. Gut contents were sorted, enumerated, and identified to the lowest possible taxon, and subsequently dried at 60°C for 24 h and weighed to the nearest 0.0001 g.

Epaxial muscle tissue was taken from Gray Triggerfish and Red Snapper (left side of the fish) and dried for 24 h at 60°C. Each tissue sample was lipid-extracted using an Accelerated Solvent Extractor (Model 300) by Dionex, as described in Plumlee and Wells (2016), and homogenized with a ball and mill grinder (Wiggle-Bug). A subsample of the resultant powder for each individual sample was then weighed (0.80 to 1.2 mg) and packaged into tin capsules. Dried filters with POM and BMA were cut in half, and edges not containing sample material were removed. Half of the filter was then weighed to the nearest mg and packaged into a tin capsule for analysis. Natural stable isotope values of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were determined using

an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer (IRMS) at the University of California-Davis Stable Isotope Facility. Stable isotope values are reported in delta notation relative to Vienna PeeDee belemnite for carbon, atmospheric nitrogen (N_2) for nitrogen, and Vienna Canyon Diablo troilite for sulfur using the following equation: where R represents the ratio of heavy to light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{34}S/^{32}S$).

$$\delta^{13}C,\ \delta^{15}N \text{ or } \delta^{34}S(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \text{ x } 1000$$

Data analysis

Gray Triggerfish and Red Snapper feeding were each examined across three age classes based on size-at-age models for Gray Triggerfish (Lombardi et al. 2015) and Red Snapper (Streich 2016). Age classes consisted of fish ages 0-1 (≤ 183 mm FL for Gray Triggerfish, and ≤ 222 mm FL for Red Snapper), 2-3 (183 to 283 mm FL for Gray Triggerfish, and 222 to 356 mm FL for Red Snapper), and 4 + (≥ 323 mm FL for Gray Triggerfish, and ≥ 357 mm FL for Red Snapper) years, hereafter referred to as juvenile, sub-adult and adult, as the majority of fish are sexually mature by age 4 for both species (SEDAR 43 2016, Kulaw et al. 2017). However, it should be noted that Gray Triggerfish reach sexual maturity faster, with some maturing by age 2 (SEDAR 43 2016). Gray Triggerfish were not caught at all sites during the study period. For this reason, analyses examining both species were restricted only to sites where they co-occurred (n = 5). All sites (n = 6) were included for analyses examining Red Snapper feeding patterns by region. Gray Triggerfish were excluded from this analysis due to low sample sizes among all regions (Table A.1). Because reef material was inconsistent among regions, observed differences in regional gut contents or stable isotopes could not be attributed to solely reef material or region. Significance was determined at an alpha value of 0.05 for all statistical analyses.

Gut contents

Gut content analyses were performed on a total of 90 Gray Triggerfish [juvenile (n = 13), sub-adult (n = 45), adult (n = 32)] and 155 Red Snapper [juvenile (n = 48), sub-adult (n = 45), adult (n = 28)] for species comparison, and an additional 140 (total n = 295) Red Snapper [juvenile (n = 64), sub-adult (n = 159), adult (n = 72)] for regional comparison. Empty guts and those solely containing unidentifiable content, chyme, bait, parasites, and inorganic material (rocks, plastic, lures) were excluded from the analysis (10% of Red Snapper and 1% of Gray Triggerfish). Identifiable contents were then categorized into 17 taxonomic groups. Several prey groups comprised less than 1% of the total dry weight (amphipods, bryozoans, echinoderms, isopods, polychaetes, sargassum, shrimp, squid, and zooplankton), thus quantitative analysis was restricted to the 8 most dominant prey groups: barnacles, bivalves, cnidarians, crabs, fish, gastropods, stomatopods, and unidentified invertebrates. Percent frequency of occurrence (% FO), percent composition by number (% N), and percent composition by weight (% W) were computed for each prey group. Likewise, a percent index of relative importance (% IRI) was calculated to integrate both weight and numerical based measures of diet following the equation by Pinkas et al. (1971):

$$\text{IRI} = \%\ \text{number} + \%\ \text{weight} \times \%\ \text{frequency of occurrence}$$

$$\%\ \text{IRI} = \left(\text{IRI}_{\text{prey item}} / \text{IRI}_{\text{total}}\right) \times 100$$

The % W of dominant prey groups was used as the dependent variable for all statistical analyses of diet, as it is a useful proxy for estimating the nutritional contribution of prey groups (Bowen 1996). Prey contributions to species diets were estimated from maximum likelihood estimates using a diet mixture model described by Moriarty et al. (2016). Because this model requires a minimum of one gut to exclusively contain the prey group of interest (making up 100 % of the % W), a reduced model (where the probability that a predator eats 100 % of the prey group was

assumed to be 0 instead of 1) was used when none of the gut samples contained 100 % of the prey (Moriarty et al. 2016). Percent composition by weight was square root transformed to reduce the importance of dominant prey groups and used to create a Bray-Curtis similarity matrix; analysis was then conducted on the resulting matrix in PRIMER v.7 (Clarke & Gorley). Permutational analysis of variance (PERMANOVA) and a posteriori tests were used to assess the effect of species and age (species comparison), and region and age (Red Snapper regional comparison) on prey group composition. Prey groups significantly differed ($p < 0.05$) across all age classes within Gray Triggerfish and between juvenile and sub-adult Red Snapper, however; the effect of species was consistent across age classes ($p < 0.05$). Regions consistently differed ($p < 0.05$) within all age classes, with exception of sub-adult and adult Red Snapper between the central and south region, likely due to small sample size (Table A.1). Age was not a significant factor ($p > 0.05$) when examining Red Snapper regional gut contents. Thus, to increase sample size, age classes were pooled for gut content analysis, and species-specific and regional differences in prey group composition were analyzed using analysis of similarity (ANOSIM). Similarity percentages (SIMPER) were used to identify prey groups with the greatest contribution to the dissimilarity between species and among regions for Red Snapper. Furthermore, the % W of family-level taxa comprising the 6 (of 8) species prey groups identified by SIMPER were examined to assess differences in taxa within these prey groups.

Stable isotopes

Ontogenetic and species-specific stable isotope values of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were examined for Gray Triggerfish [juvenile (n = 12), sub-adult (n = 44), and adult (n = 33)] and Red Snapper [juvenile (n = 53), sub-adult (n = 92), and adult (n = 37)] using multivariate analysis of variance (MANOVA), with $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ as dependent variables, and species and age as independent variables. The influence of ontogeny and species were then

independently examined for each dependent variable ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) using univariate analysis of variance (ANOVA). Pairwise differences among means were examined using the Shaffer procedure (Shaffer 1986, Bretz et al. 2016), as it is less affected by unbalanced sample sizes than other post hoc tests and still controls for Type I error. Similarly, MANOVA was used to compare regional and age-specific differences in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ for Red Snapper [north (n = 203), central (n = 83), south (n = 41)]. ANOVA models were then used to examine the influence of ontogeny and region on each dependent variable ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$); pairwise differences among means were obtained using the Shaffer procedure. Lastly, MANOVA was used to test for regional differences in source, POM [north (n = 3), central (n = 6), south (n = 3)] and BMA [north (n = 3), central (n = 6), south (n = 0)], isotope values, with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables. Statistical analyses were performed in R (R Core Team 2017) using the mult-comp package (Hothorn et al. 2008).

Isotopic niches

Population metrics, including the mean distance to centroid and stable isotope ($\delta^{13}C$ and $\delta^{15}N$ and $\delta^{34}S$) ranges (Layman et al. 2007, Jackson et al. 2012), and standard ellipse areas were computed (using individual species stable isotope values) using Stable Isotope Bayesian Ellipses in R (SIBER) to examine isotopic niche and niche overlap between species and among regions (Jackson et al. 2011). Analyses were performed within each age class and using age class combined data. To account for isotopic relationships with size for the age class combined analysis (Boecklen et al. 2011), values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ were length adjusted according to the following equation (Melville & Connolly 2003), where $\delta X'$ = adjusted isotope values, δX = raw isotope value, a = regression coefficient, and FL = fork length of fish (mm).

$$\delta X' = \delta X - (a\ x\ FL)$$

Standard ellipse areas (SEA), representing a group's core isotopic niche, were calculated for each species, age class, and region. To minimize bias due to small sample size, SEA was subsequently corrected to SEA_c (Jackson et al. 2012), representing SEA adjusted for small sample size, and then used to calculate potential isotopic niche overlap. Overlap between ellipses was considered significant if ≥ 0.60, representing 60% overlap between two groups SEA_c's (Schoener 1968, Guzzo et al. 2013). Credible intervals were then obtained for isotopic niche areas for statistical comparison using a Bayesian technique detailed in Jackson et al. (2011). In addition, population metrics were calculated based on the individuals used to determine isotopic niche areas. The mean distance to centroid (CD) serves as a measure of group trophic diversity, while nitrogen range (NR) and carbon range (CR) represent the ranges of $\delta^{13}C$ and $\delta^{15}N$ exploited by each species (Layman et al. 2007). The sulfur range (SR) was calculated in the same manner as NR and CR. Sample size varied for species and regions, thus population metrics (CD, NR, CR, SR) were bootstrapped (n = 10,000) based on the group with the smallest sample size (n = 89 for Gray Triggerfish, and n = 41 for Red Snapper in the south region) for statistical comparison based on resultant confidence intervals.

Source contributions

Relative contributions of pelagic (POM) and benthic (BMA) carbon to the diets of juvenile, sub-adult, and adult Gray Triggerfish and Red Snapper were estimated using Bayesian mixing models in MixSIAR (Stock & Semmens 2013). Individual species stable isotope values were used with trophic discrimination factors of 1.00 ‰ ± 0.30 SD for $\delta^{13}C$, and 3.00 ‰ ± 0.60 SD for $\delta^{15}N$ (Rooker et al. 2006, Wells et al. 2017). Trophic level for each species and age class was calculated according to Post (2002):

$$\text{trophic level} = 1 + (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{prod}})/\Delta_{\text{n}}$$

where $\delta^{15}N_{fish}$ is the $\delta^{15}N$ value of an individual consumer (Gray Triggerfish or Red Snapper), $\delta^{15}N_{prod}$ is the mean $\delta^{15}N$ value of the primary producers [POM (n = 12), BMA (n = 9)], and Δ_n is the trophic discrimination factor for each trophic level. Models in MixSIAR were not concentration dependent, and comprised both residual and process error with 100,000 (50,000 burn-ins) iterations for all Gray Triggerfish age classes and juvenile Red Snapper. Models for sub-adult and adult Red Snapper were comprised of 300,000 iterations (200,000 burn-ins) due to failure to converge using 100,000 (50,000 burn-ins) iterations. To verify model convergence, Gelman-Rubin diagnostics were used (Gelman & Rubin 1992).

RESULTS

Species comparison

Analysis of Gray Triggerfish and Red Snapper gut contents indicated species-specific differences in primary prey groups (Table A.2). Prey groups (identified by SIMPER) most responsible for differentiation between species diets were crabs, unidentified invertebrates, bivalves, fish, gastropods, and stomatopods. Estimated prey contributions to species diets from the Diet Mixture Model identified crabs [24 % ± 2.94 SE ($\bar{x}$ ± SE)], unidentified invertebrates (18 % ± 2.93), bivalves (14 % ± 2.37), and gastropods (14 % ± 2.79) as the largest contributors to the diets of Gray Triggerfish. Similarly, prey groups with the highest % IRI for Gray Triggerfish were gastropods, crabs and bivalves (Figure A.2). In contrast, the greatest estimated prey contributions for Red Snapper were crabs (27 % ± 4.06), stomatopods (21 % ± 4.31), fish (15 % ± 3.1), and unidentified invertebrates (14 % ± 3.37). In addition, crabs, unidentified invertebrates, and fish had the highest % IRI for Red Snapper. Constituent family-level taxa comprising prey groups identified by SIMPER varied by species, with Gray Triggerfish consuming more xanthid crabs (17.02 % vs. 1.22 %) and Red Snapper consuming more portunid crabs (7.27 % vs. 2.75 %, Table A.3). Likewise, Gray Triggerfish consumed more pelagic gastropods from family Cavolinidae (9.93 % vs. 0.46 %) than Red Snapper (Table A.3). Although sample size was low within species age classes, differences between species diets were consistent when examined within juvenile, sub-adult, and adult fishes ($p > 0.05$, two-way PERMANVOA).

The effect of species on stable isotope values was significant across all age classes (Table A.4, Figure A.3A) where Gray Triggerfish had significantly lower $\delta^{13}C$ ($\bar{x}$ difference = 0.56 ‰) and $\delta^{15}N$ ($\bar{x}$ difference = 2.30 ‰) values compared to Red Snapper ($p < 0.05$,

ANOVA). Gray triggerfish $\delta^{34}S$ values were generally higher than those for Red Snapper; but were highly variable, with no significant difference between species ($p > 0.05$, ANOVA). Ontogenetic shifts were observed for both species, with a general trend of increasing $\delta^{13}C$ and $\delta^{15}N$ values with size (Figure A.3A). Sub-adult Gray Triggerfish $\delta^{13}C$ and $\delta^{15}N$ values, -17.48 ‰ ± 0.09 and 14.16 ‰ ± 0.23, respectively, were significantly higher than for juveniles ($\delta^{13}C$ = -18.23 ‰ ± 0.14, $\delta^{15}N$ = 12.48 ‰ ± 0.23) ($p < 0.05$, ANOVA). The same was observed for Red Snapper, where sub-adult $\delta^{13}C$ (-17.13 ‰ ± 0.02) and $\delta^{15}N$ (16.22 ‰ ± 0.07) values were significantly higher than $\delta^{13}C$ and $\delta^{15}N$ for juveniles, -17.34 ‰ ± 0.04 and 15.79 ‰ ± 0.06, respectively ($p < 0.05$, ANOVA) (Figure A.3A).

Isotopic niches and population metrics for age class combined Gray Triggerfish and Red Snapper significantly differed. Gray Triggerfish had a larger isotopic niche (SEA_c) as well as greater and wider ranging population metrics (CD, CR, NR, and SR) (Table A.5). The SEA_c for Gray Triggerfish was significantly larger than for Red Snapper (Figures A.4 & A.5), with no significant overlap between species core isotopic niches (Table A.5). Trophic diversity was also significantly greater for Gray Triggerfish than for Red Snapper based on CD bootstrapped confidence intervals (Table A.5). Likewise, Gray Triggerfish utilized a significantly wider range of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ than Red Snapper (based on CR, NR, and SR bootstrapped confidence intervals), indicating a greater diversity of pelagic vs. benthic prey and greater trophic diversity for Gray Triggerfish. Results for species isotopic niches and population metrics (CD, CR, NR, and SR) within juvenile, sub-adult, and adult fishes showed the same trends as the age class combined analyses.

Source contribution estimates from the Bayesian two-source mixing models were species-specific and varied with ontogeny. Source $\delta^{13}C$ values significantly differed between POM (-22.50 ‰ ± 0.13) and BMA (-18.80 ‰ ± 0.20) ($p < 0.05$, Student's t-test), while $\delta^{15}N$

values were similar, 6.03 ‰ ± 0.31for POM (pelagic carbon) and 5.27 ‰ ± 0.35 for BMA (benthic carbon). Pelagic as well as benthic carbon sources contributed to both Gray Triggerfish and Red Snapper (Figure A.6). Contributions from benthic carbon were slightly higher than pelagic for both species across all age classes ($\bar{x}$ difference = 21.60 %), except for juvenile Gray Triggerfish, for which pelagic contribution estimates were highest (60.00 % ± 7.00 SD). Benthic carbon contribution increased with ontogeny for both species, with contributions increasing by ~18 % and ~2 % for sub-adult and adult Gray Triggerfish and ~3 % and ~10 % for sub-adult and adult Red Snapper, respectively. In addition, sub-adult and adult Gray Triggerfish had higher contributions from pelagic sources than Red Snapper within the same age classes ($\bar{x}$ difference = 6.00 %). Pelagic and benthic sources were highly correlated (negative) in the diagnostic matrix plots of the posterior distributions for the models, which may be indicative of a missing source/primary producer (i.e., red algae, green algae, epiphytes), or too small of a difference in pelagic vs. benthic $\delta^{13}C$ and $\delta^{15}N$ to be effectively differentiated in the model.

Regional comparison

Water parameters (bottom measurements) and primary producers (POM, BMA) $\delta^{13}C$ and $\delta^{15}N$ values were compared to assess possible regional differences. Salinity and temperature were similar across the three regions (north, central, south) ($p > 0.05$, MANOVA). Salinity was lowest in the north (34.07 ± 0.76), and progressively increased in the central (35.78 ± 0.61) and south (36.07 ± 0.95) regions. Mean temperatures in the north, central and south regions were 28.19 °C ± 1.04, 29.19°C ± 0.61, and 27.73 °C ± 1.12, respectively. Dissolved oxygen was 7.37 mg l-1 ± 0.62, 6.84 mg l-1 ± 0.51, and 7.10 mg l-1 ± 0.79, listed north to south. Primary producer (POM, BMA) $\delta^{13}C$ and $\delta^{15}N$ values were similar across regions ($p > 0.05$, MANOVA). POM $\delta^{13}C$, from north to south, was -22.51 ‰ ± 0.07, -22.82 ‰ ± 0.12, and -22.30 ‰ ± 0.42, respectively, and $\delta^{15}N$ was 5.23 ‰ ± 0.75, 6.66 ‰ ± 0.23, and 5.95 ‰ ± 0.99. Regional BMA

$\delta^{13}C$ was also similar between the north (-19.32 ‰ ± 0.23) and central (-18.66 ‰ ± 0.24) regions, as was BMA $\delta^{15}N$ values (north: 6.20 ‰ ± 0.40, central: 4.80 ‰ ± 0.37). Due to failed sampling attempts, BMA was not collected from the south region. However, BMA stable isotope values did not differ between the north and central regions, and were comparable to previous reports throughout the GoM (Moncreiff & Sullivan 2001, Daigle et al. 2013). Thus, BMA stable isotope values in the south region were assumed to be comparable to what we found for the north and central regions.

Analysis of Red Snapper gut contents indicated differences in primary prey groups across regions (Table A.2). Prey groups most responsible for regional differences in Red Snapper diets were crabs, unidentified invertebrates, stomatopods, and fish. Crab consumption in the north region increased by 50 and 77 % compared to the central and south regions, respectively. In contrast, consumption of stomatopods was highest (73 - 79 %) in the central region, and consumption of fishes (36 - 52 %) and unknown invertebrates (22 - 31 %) was highest in the south region. Region-specific prey contribution estimates to Red Snapper diets were similar across all three regions, with estimates being consistently highest for crabs (26 - 39 %), other invertebrates (15 - 20 %), fishes (3 - 9 %), and stomatopods (1 - 2 %), suggesting that these prey groups are similarly important to the diet across all regions. Differences in gut contents across regions were consistent when examined within juvenile, sub-adult, and adult fish ($p < 0.05$, two-way PERMANOVA), with exception of sub-adults and adults in the central and south regions, which were not significantly different ($p > 0.05$, two-way PERMANOVA). This is likely due to small regional sample sizes within these age classes (Table A.1).

Red Snapper $\delta^{13}C$ and $\delta^{15}N$ values generally decreased from north to south, while $\delta^{34}S$ increased across this gradient (Table A.4, Figure A.3B). All age classes of Red Snapper in the north region had significantly higher $\delta^{13}C$ values ($\bar{x}$ difference = 0.27 ‰) than the central and

south regions ($p < 0.05$, ANOVA), in addition to higher $\delta^{15}N$ ($\bar{x}$ difference = 1.28 ‰) values for sub-adult and adult fish ($p < 0.05$, ANOVA). In contrast, $\delta^{34}S$ values in the north were significantly lower across all age classes ($p < 0.05$, ANOVA). Red Snapper in the south region had significantly lower $\delta^{13}C$ values across all age classes relative to the north and central regions ($p < 0.05$, ANOVA), and significantly higher $\delta^{34}S$ values ($p < 0.05$, ANOVA). $\delta^{15}N$ values for south sub-adult (15.71 ‰ ± 0.29) and adult Red Snapper (14.69 ‰ ± 0.39) were significantly lower than sub-adults in the north (15.93 ‰ ± 0.06) ($p < 0.05$, ANOVA), as well as adults from the north (17.05 ‰ ± 0.04) and central (16.13 ‰ ± 0.09) regions ($p < 0.05$, ANOVA). Ontogenetic trends for Red Snapper were similar within the north and central regions, where both $\delta^{13}C$ and $\delta^{15}N$ increased ($\bar{x}$ difference = 0.18 ‰) from juvenile to sub-adult fish ($p < 0.05$, ANOVA). In the north region, $\delta^{15}N$ also increased between sub-adult (16.74 ‰ ± 0.03) and adult fish (17.05 ‰ ± 0.04) ($p < 0.05$, ANOVA). Interestingly, the opposite trend with ontogeny was observed for Red Snapper $\delta^{15}N$ values in the south region, as no difference was observed between juvenile and sub-adult fish, and adult (14.69 ‰ ± 0.40) fish significantly decreased in $\delta^{15}N$ from sub-adults (15.71 ‰ ± 0.29) ($p < 0.05$, ANOVA). Isotopic niches (encompassing all age classes) showed no significant overlap between regions (Table A.5). While isotopic niches for the north (0.16) and central (0.20) regions were similar in size, isotopic niche size in the south region (0.62) was significantly larger (Figures A.4 & A.5). Likewise, Red Snapper from the south region had greater trophic diversity (based on bootstrapped confidence intervals) and exploited a larger (based on bootstrapped confidence intervals) range of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ than Red Snapper from the north and central regions (Table A.5). Regional isotopic niches and population metrics (CD, CR, NR, SR) within juvenile, sub-adult, and adult fish were consistent with the results of the age class combined analyses.

CONCLUSIONS

Gray Triggerfish and Red Snapper are generalists (Tarnecki & Patterson 2015, Goldman et al. 2016) and demonstrated diverse diets at artificial reef sites in the Northwest GoM, with 66 unique prey identified in Gray Triggerfish and 47 in Red Snapper. The two species consumed similar prey groups; however, relative contributions and family-level composition of taxa within these groups differed greatly, suggesting prey partitioning between species. Crabs represented the most important prey group for both species, although differences were observed in the types of crabs consumed, with xanthid crabs more common for Gray Triggerfish and portunid crabs for Red Snapper. Likewise, the prominence of bivalves and pelagic gastropods in the diets of Gray Triggerfish relative to Red Snapper, suggests differences in foraging behavior, where Gray Triggerfish may feed on pelagic and benthic prey more regularly.

Observed diets of both species were consistent with previous studies examining Gray Triggerfish and Red Snapper feeding. Gray Triggerfish diets were similar to reports from the southeastern United States identifying gastropods, decapods, bivalves, and barnacles as primary prey groups (Vose & Nelson 1994, Goldman et al. 2016). Likewise, Gray Triggerfish are known to consume large numbers of pelagic gastropods (pteropods, Goldman et al. 2016), which is in agreement with the majority of identified gastropods in Gray Triggerfish guts being pelagic taxa (e.g. Cavolinidae, Atlantidae, and Limacinidae). In the GoM, reports on Gray Triggerfish feeding consist of observations of sand dollar predation (Frazer et al. 1991,Vose & Nelson 1994, Kurz 1995), but were absent in the gut contents of this study. For Red Snapper, the predominance of stomatopods and fishes in the diet agrees with other studies in the GoM examining similar sized individuals (Szedelmayer & Lee 2004, Wells et al. 2008, Tarnecki & Patterson 2015). However, this study differed from others in that, while identified in the gut

contents, squid were not a primary contributor to the diet. Because Red Snapper are highly opportunistic foragers (Tarnecki & Patterson 2015), this is likely due to differences in local prey abundances at our sites in comparison to those sampled in other studies. Reports of squid as a prominent prey group in Red Snapper (Szedelmayer & Lee 2004, Wells et al. 2008) included fall and winter sampling, while this study focused around spring and summer months. Furthermore, Wells et al. (2008) found squid to be more important in the fall and winter, while fishes were more prominent during the summer.

Sessile taxa associated with hard substrate were more commonly consumed by Gray Triggerfish, with several taxa being unique to their diet. While Gray Triggerfish and Red Snapper consumed both sessile and mobile prey, the greater diversity and proportion of sessile organisms (i.e. reef-attached) in Gray Triggerfish (i.e. Barnacles, Bivalves: Mytilidae, Plicatulidae, Pteriidae, Chamidae, and Campanulariidae) guts indicates more frequent foraging on the reef structure. Gray Triggerfish possess unique dentition and jaw morphology that is suitable for consuming hard-bodied sessile organisms (Vose & Nelson 1994), which possibly enables greater feeding opportunities on reef-attached organisms compared to Red Snapper. While Red Snapper also fed on some families of bivalves, they contributed relatively little to the overall diet. Greater consumption of fishes, stomatopods, and portunid crabs, which are associated with open mud and/or sand bottom (Szedlmayer & Lee 2004, Wells et al. 2008), indicates that Red Snapper likely feed at a higher trophic level, and may depend more on non-reef prey surrounding artificial reefs.

Consumer $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values were useful for reconstructing feeding patterns and discerning trophic interactions. Muscle tissue $\delta^{13}C$ values for Gray Triggerfish and Red Snapper were comparable to those previously reported in the GoM, while $\delta^{15}N$ values were slightly higher. Reported $\delta^{13}C$ values for Gray Triggerfish at artificial reefs are limited, but

values based off small sample sizes (n = 4, -17.83 ‰ ± 0.55 SE, Daigle et al. 2013) were similar to results of the current study (-17.61 ‰ ± 0.06 SE). Likewise, Red Snapper $\delta^{13}C$ values (-17.19 ‰ ± 0.02 SE) were similar to those previously reported at artificial reefs off the Texas coast (Zapp-Sluis et al. 2013). In contrast, $\delta^{15}N$ values for Red Snapper were higher compared to other regions in the GoM (~15 ‰); however, these studies found significant contribution from zooplankton to Red Snapper diets (Tarnecki & Patterson 2015), which were not major contributors to the diets in this study. Species $\delta^{34}S$ values were comparable to consumers in other marine systems (16 - 18 ‰) where the substrate (course and fine sands) was similar to that surrounding the reef sites in the current study (Fry 1988). Lower $\delta^{13}C$ and $\delta^{15}N$ values for Gray Triggerfish relative to Red Snapper across all age classes may be due to more frequent foraging on lower trophic level prey, such as filter feeding benthic invertebrates (bivalves) and pteropods, and this is supported by generally higher $\delta^{34}S$ values (although non-significant) for Gray Triggerfish. Red Snapper were far more piscivorous than Gray Triggerfish and would be expected to occupy a higher trophic level, as species that consume large amounts of fish generally have higher $\delta^{15}N$ values than species primarily consuming invertebrate prey (Fry 2007). Increases in $\delta^{13}C$ and $\delta^{15}N$ values with age class for Gray Triggerfish and Red Snapper were consistent with studies examining ontogenetic shifts in diet (Szedlemayer & Lee 2004, Wells et al. 2008). $\delta^{34}S$ values decreased with ontogeny; however variation was likely too large to detect significant differences. This is well documented as rapid increases in body size enables fish to consume a greater diversity of prey items, especially in the first few years of life when growth is accelerated (Herzka & Holt 2000, Wells et al. 2008, Boecklen et al. 2011).

Assessment of species isotopic niches indicated more diverse prey and greater trophic diversity for Gray Triggerfish than for Red Snapper. Gray Triggerfish had a larger isotopic niche and greater values for all population metrics (CD, CR, NR, SR), suggesting a more diverse diet,

encompassing both pelagic and benthic prey. This finding is consistent with the greater number of taxon identified in Gray Triggerfish gut contents relative to Red Snapper, as well as other studies that describe Gray Triggerfish as a flexible forager with a wide niche breadth (Vose & Nelson 1994, Ballard et al. 2012, Goldman et al. 2016). Interestingly, despite similar contribution estimates for crabs in species' diets, no significant overlap was observed, which is likely due to family-level taxonomic differences in diet not accounted for in the broader prey categories, such as the greater proportion of xanthid crabs in Gray Triggerfish and portunid crabs in Red Snapper (Vose & Nelson 1994, Szedlmayer & Lee et al. 2004, McCawley et al. 2006, Tarnecki & Patterson 2015). In addition, xanthid crabs are more frequently associated with reefs, while portunid crabs are more associated with the sand and mud substrates surrounding the reef (Szedlmayer & Lee 2004, McCawley et al. 2006, Wells et al. 2008).

Source contribution estimates are important for understanding energy flow and identifying essential resources to consumers at artificial reefs. Stable isotope values of POM and BMA were comparable to previously reported values in the GoM, where $\delta^{13}C$ and $\delta^{15}N$ values ranged from, -19.00 to -22.00 ‰ and 5.00 to 7.00 ‰ for POM, and from -14.70 to -19.90 ‰ and 6.70 to 7.80 ‰ for BMA, respectively (Moncreiff & Sullivan 2001, Wells et al. 2008, Daigle et al. 2013). Previous estimates of source contributions for adult Gray Triggerfish are limited (estimates of POM for 4 individuals, Daigle et al. 2013), as this study represents the first comprehensive contribution estimates for both POM and BMA to this species. While results show the importance of both pelagic and benthic carbon to Gray Triggerfish, pelagic contribution estimates presented here (~41 %) were similar to those described at offshore oil and gas platforms (~37 %, Daigle et al. 2013). This study is in accord with findings from Wells et al. (2008) that highlighted the importance of both pelagic and benthic primary production to Red Snapper at artificial reefs. Likewise, the previous study demonstrated increases in benthic

contributions to Red Snapper with age (34 - 51% from age 1 - 3, Wells et al. 2008), which corroborates observed increases in the influence of benthic primary production with ontogeny for Gray Triggerfish and Red Snapper as they became more reef- associated (Gallaway et al. 2009). Gray Triggerfish and Red Snapper had significant contributions from both pelagic and benthic sources; however, benthic contribution estimates were greater for both species within all age classes (except juvenile Gray Triggerfish), suggesting that benthic primary production may be important for consumers at artificial reefs. Higher pelagic contribution estimates relative to benthic contributions for juvenile Gray Triggerfish may be reflective of species-specific differences in the timing of a shift from pelagic to benthic habitat during juvenile life stages (Gallaway et al. 2009, Simmons & Szedlmayer 2011). Juvenile Gray Triggerfish recruit to benthic habitats much later (4-7 months, Simmons & Szedlmayer 2011) than Red Snapper (~30 days, Rooker et al. 2004), and are thus more likely to reflect feeding in the pelagic environment due to limited time for tissue turnover, which can take weeks in juveniles and up to a year in older, slower growing adults (Herzka & Holt 2000, Herzka 2005, Nakamura et al. 2008). Despite the importance of benthic carbon to older fish of both species, pelagic contribution was slightly higher for Gray Triggerfish at all age classes, supporting the importance of filter feeding invertebrates to the diet of this species. However, mixing model diagnostics suggest a potential missing source (i.e., red algae, green algae, epiphytes), thus contribution estimates from pelagic and benthic sources may have differed if other potential sources of primary production had been incorporated.

Diets of Red Snapper across three regions (north, central, south) indicated pronounced regional differences in feeding. These differences are likely due to a combination of environmental factors that differed among regions (depth, structure, physiochemical properties), and are known to affect reef fish communities (Bortone et al. 1998, Strelcheck et al. 2005, Lingo

& Szedlmayer 2006, Jaxion-Harm & Szedlmayer et al. 2015). Although we did not directly assess regional assemblages, reef material and complexity have been shown to play a significant role in reef fish demographics (Bortone et al. 1998, Strelcheck et al. 2005, Lingo & Szedlmayer 2006) and this likely affects prey communities as well. In addition, it is possible that regional differences in freshwater inflow may have resulted in spatial variation in prey communities among the artificial reefs investigated. While water parameters were similar during the season in which we sampled (summer), regional differences exist when examined over all seasons, as there is a known north to south salinity gradient along the Texas coast (Tolan 2007). The larger isotopic niche and differing ontogenetic trend in $\delta^{15}N$ for Red Snapper in the south suggests a shift to more pelagic feeding for larger fish, similar to studies that reported an increase in zooplankton consumption with size (Tarnecki & Patterson 2015). While zooplankton were not primary contributors to the diet, sample size for guts in the south region (n = 34) was small and contained the largest individuals (> 500 mm TL). In addition, the southern reefs had unique, complex structures not found in the other regions (ships), and it has been shown that more complex reefs attract a greater number of fishes (Bortone et al. 1991) and increase species diversity and richness (Lingo & Szedlmayer 2006), which could affect prey composition and availability through differing rates of predation. While we did not collect prey at our sites, inshore fishes, characteristic of lower salinities were more commonly caught as bycatch in the north and central regions (catfish, drums), while more diverse reef fish communities were observed at the more complex sites in the south region, suggesting that fish and prey communities in the south were more diverse.

This study examined the trophic interactions and feeding ecology of two of the most common reef fish species at artificial reefs in the Northwest GoM. Results highlight the importance of pelagic and benthic primary production to upper-level consumers at artificial

reefs, and demonstrate that Gray Triggerfish and Red Snapper exhibit some degree of resource partitioning. Although Gray Triggerfish feed on benthic (bivalves, crabs) and pelagic (pteropods) prey, the diet of this species was more dependent on organisms associated with the actual reef structure. Red Snapper occupied a higher trophic level than Gray Triggerfish, and consumed prey primarily associated with the surrounding substrate, which suggests less direct dependence on the reef itself for foraging opportunities. Regionally, Red Snapper gut contents and stable isotopes indicated differences in diet across all three regions, with additional differences in niche width and ontogeny in the south region. Although the effects of depth and structure were not able to be assessed in this study, artificial reef literature and regional site characteristics suggest that prey communities may have differed across our study area, contributing to these differences. Outcomes were consistent with other feeding studies showing the importance of pelagic and benthic primary production at artificial reefs (Lindquist et al. 1994, Wells et al. 2008). In addition, partitioning of resources (prey) by two of the most abundant reef fish species at artificial reefs in the GoM suggests that a diversity of resources is likely important to supporting reef fish assemblages with a diversity of species and age classes. Findings also highlight the need for future studies aimed at examining the feeding ecology of fishes and invertebrates at artificial reefs at the community level to better understand the trophic dynamics and ecological function of these systems.

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APPENDIX

Tables and figures

Table A.1: Gray Triggerfish and Red Snapper sample sizes for gut content and stable isotope analyses by age class and region (Red Snapper only).

	Gut contents			Stable Isotopes		
	North	**Central**	**South**	**North**	**Central**	**South**
Species Comparison						
Red Snapper						
Juveniles	15	16	17	15	19	19
Sub-adults	31	37	11	33	44	15
Adults	12	10	6	15	15	7
Gray Triggerfish						
Juveniles	3	2	8	3	2	7
Sub-adults	20	22	3	20	21	3
Adults	9	8	15	9	8	16
Regional Comparison						
Red Snapper						
Juveniles	28	19	17	28	22	19
Sub-adults	109	39	11	115	46	15
Adults	56	10	6	60	15	7

Table A.2: Analysis of similarity (ANOSIM) examining gut contents by species, Gray Triggerfish (n = 90) and Red Snapper (n =155) and region (Red Snapper), north (n = 193), central (n = 68), and south (n = 34). Percent dissimilarity between groups is additionally shown from similarity percentages (SIMPER).

ANOSIM pairwise tests	***Global R***	**p-value**	**Dissimilarity (%)**
Species Comparison			
Gray Triggerfish vs. Red Snapper	0.059	0.003	76.36
Regional Comparison			
North vs. Central	0.278	0.001	72.97
North vs. South	0.429	0.001	78.70
Central vs. South	0.085	0.005	80.79

Table A.3: Percent weight (%W) of constituent taxa (family-level) for prey groups that contributed most to the dissimilarity in diet between species, Gray Triggerfish (n = 90) and Red Snapper (n = 155).

Prey Group	Gray Triggerfish %W	Red Snapper %W
Crabs		
unknown crabs	3.47	12.71
Porcellanidae	0.12	0.18
Paguroidea	0.44	0
Hepatidae	1.22	0
Leucosiidae	0.54	1.99
Portunidae	2.75	7.27
Xanthoidea	17.02	1.22
Total	25.56	23.37
Unidentified Invertebrates		
Total	19.90	14.79
Bivalves		
unknown bivalves	2.11	4.46
Arcidae	8.25	0.04
Crassatellidae	0	0.17
Corbulidae	0	0.06
Mytilidae	8.81	0
Plicatulidae	0.11	0
Pteriidae	0.61	0
Chamidae	0.87	0
Veneridae	0.35	0
Total	21.11	4.73
Fishes		
unknown fish	9.90	24.32
Syngnathidae	0	0.01
Blenniidae	0	0.57
Total	9.90	24.9
Gastropods		
unknown gastropods	1.54	0.02
Atlantidae	0.03	0
Collumbellidae	0.03	0.01
Nassariidae	0	0.04
Fissurellidae	0.08	0
Limacinidae	0.01	0
Natcidae	0.07	0.01
Pyramidellidae	.01	0
Hipponicidae	.10	0
Cavolinidae	9.93	0.46
Lottidae	0.02	0
Total	11.82	0.54
Stomatopods		
Squillidae	0.15	31.27
Total	0.15	31.27

Table A.4: Multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA) results examining differences in $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ by species, age, and region (Red Snapper). A total of 89 Gray Triggerfish [juvenile (n = 12), sub-adult (n = 44), adult (n = 33)] and 182 Red Snapper [juvenile (n = 53), sub-adult (n = 92), adult (n =37)] were used for comparison of species, while a total of 327 Red Snapper were used for regional comparison [north (n = 203), central (n = 83), south (n = 41)].

Factor	df	*F*-value	p-value
Species Comparison			
MANOVA: (C, N, & S)			
Species	3	160.86	< 0.001
Age	6	9.97	< 0.001
ANOVA: species			
$\delta^{13}C$	1	82.04	< 0.001
$\delta^{15}N$	1	281.04	< 0.001
$\delta^{34}S$	1	3.15	0.077
ANOVA: age			
$\delta^{13}C$	2	17.96	< 0.001
$\delta^{15}N$	2	17.44	< 0.001
$\delta^{34}S$	2	2.92	0.056
Regional Comparison			
MANOVA: (C, N, & S)			
Region	6	68.74	< 0.001
Age	6	13.79	< 0.001
ANOVA: region			
$\delta^{13}C$	2	129.49	< 0.001
$\delta^{15}N$	2	186.69	< 0.001
$\delta^{34}S$	2	41.58	< 0.001
ANOVA: age			
$\delta^{13}C$	2	22.66	< 0.001
$\delta^{15}N$	2	29.61	< 0.001
$\delta^{34}S$	2	1.13	0.056

Table A.5: Population metrics used for assessing species [Gray Triggerfish (n = 89), Red Snapper (n = 182)] and Red Snapper regional [north (n = 203), central (n = 83), south (n = 41)] isotopic niches. Standard ellipse area (SEA), corrected for sample size (SEA_c) is shown along with mean distance to centroid (CD), $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ ranges (CR, NR, SR), and the proportion overlap between groups' SEA_c. Overlap (SIBER) between ellipses was considered significant if ≥ 0.6 (Schoener 1968).

Analysis	**SEA_c**	**CD**	**$\delta^{13}C$ Range**		**$\delta^{15}N$ Range**		**$\delta^{34}S$ Range**		**Overlap**
			Min	Max	Min	Max	Min	Max	
Species Comparison									
Red Snapper	0.45	0.43	-18.54	-17.01	12.37	16.18	17.91	20.26	< 0.0001
Gray Triggerfish	1.93	0.74	-19.15	-16.65	7.61	15.08	17.24	20.55	
Regional Comparison									
North Central	0.16	0.30	-17.84	-16.95	14.62	16.44	17.85	19.69	0.0006
Central South	0.20	0.34	-17.90	-17.01	13.72	15.90	18.02	19.68	0.0010
South North	0.62	1.01	-18.54	-17.35	12.37	16.18	18.07	20.26	0.0059

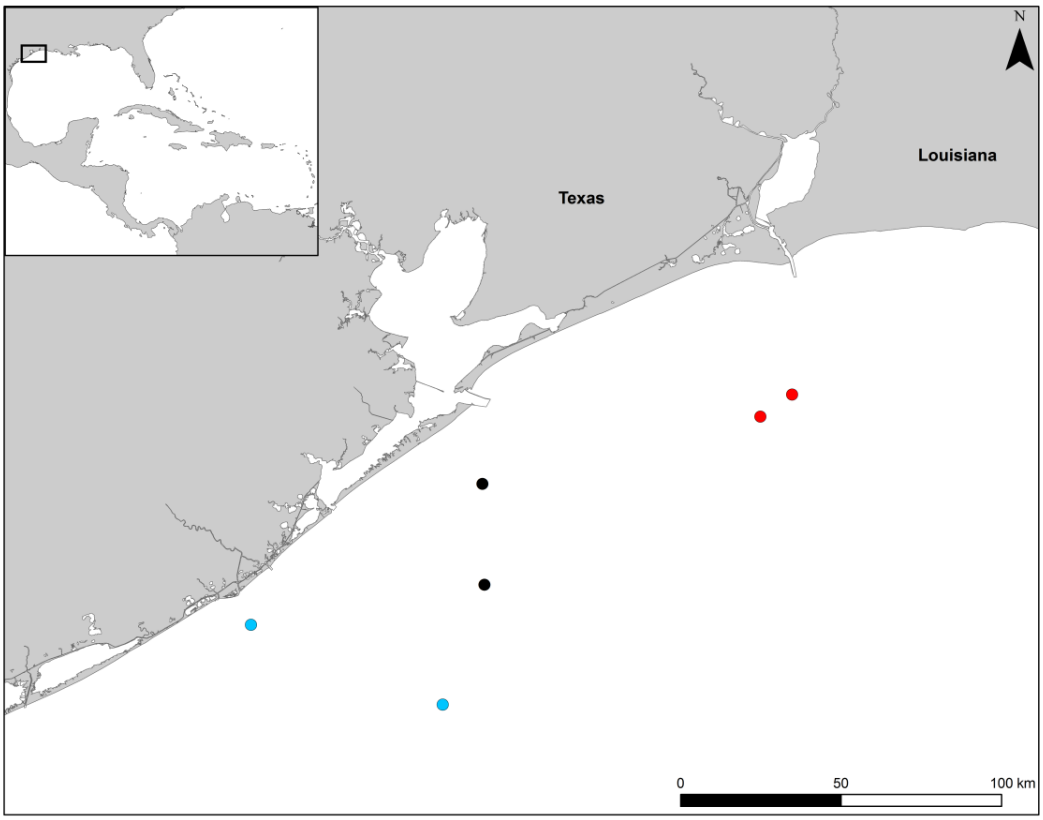

Figure A.1: Location of study sites off the Texas coast in the Northwest Gulf of Mexico. Reefs were grouped into three regions, north (n = 2, red), central (n = 2, black) and south (n = 2, blue).

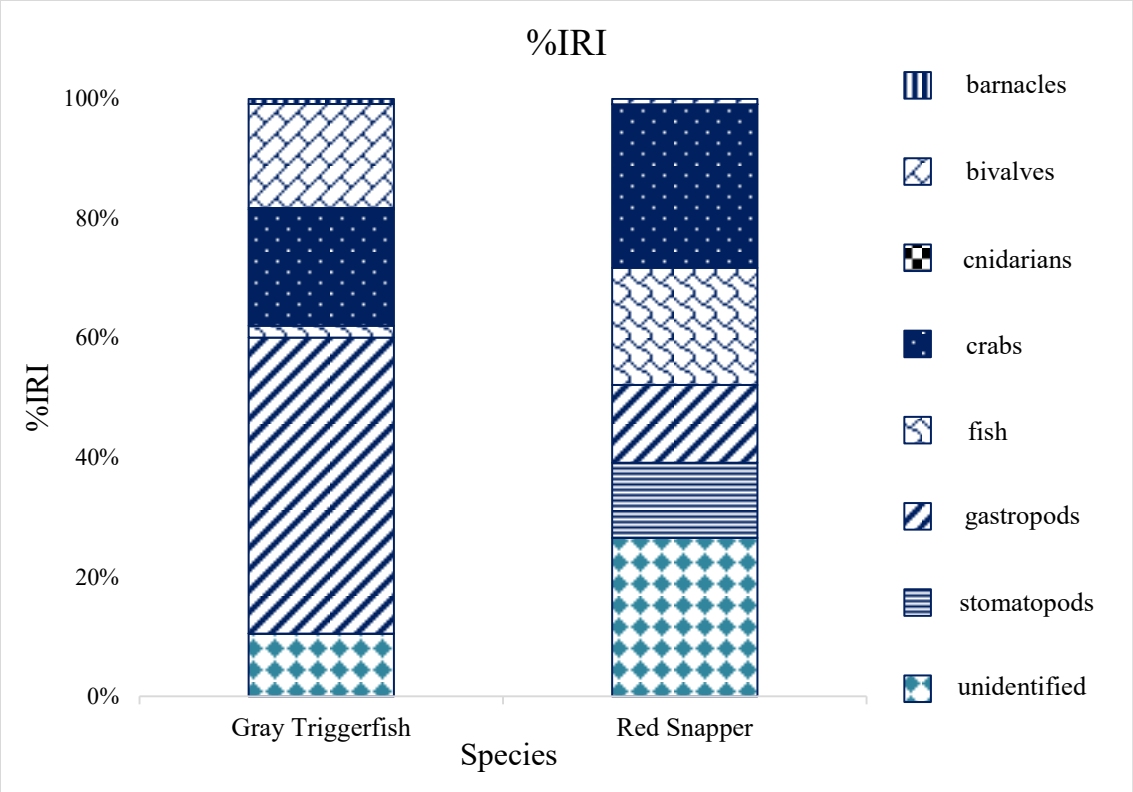

Figure A.2: Percent index of relative importance (%IRI) for prey groups accounting for more than 1% of the total percent weight (%W) in Gray Triggerfish (n = 90) and Red Snapper (n = 155) gut contents.

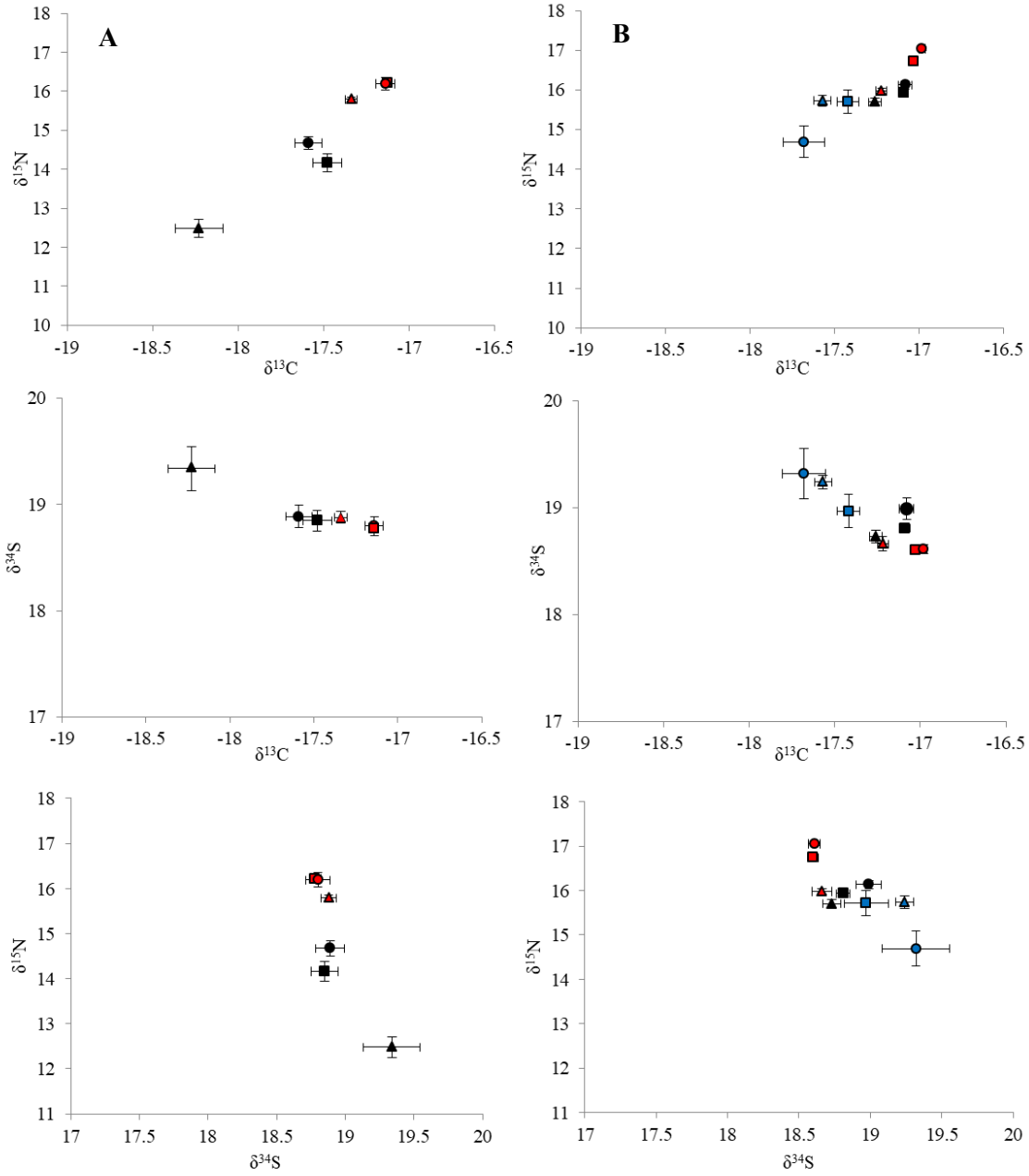

Figure A.3: Mean stable isotope biplots for **Column A:** Gray Triggerfish (black) and Red Snapper (red) and **Column B:** north (red), central (black), and south (blue) Red Snapper. Juvenile (triangles), sub-adult (squares) and adult (circles) fish are shown; error bars represent the standard error.

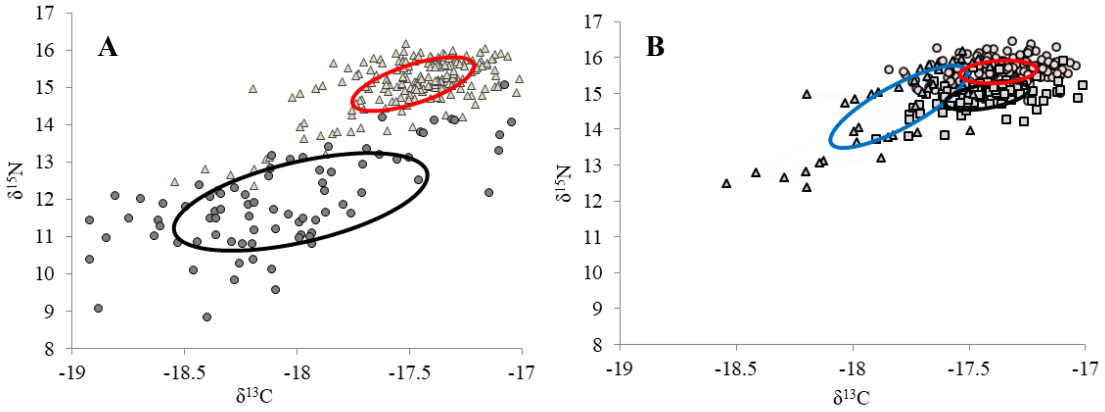

Figure A.4: Stable isotope bi-plots depicting core isotopic niches based on standard ellipse areas (SEA_c), containing 40% of the data, for **A:** Species, Gray Triggerfish (circles, black ellipse) and Red Snapper (triangles, red ellipse), and **B:** Region (Red Snapper), north (circles, red ellipse), central (squares, black ellipse) and south (trianges, blue ellipse). Points represet length-adjusted individual stable isotope values.

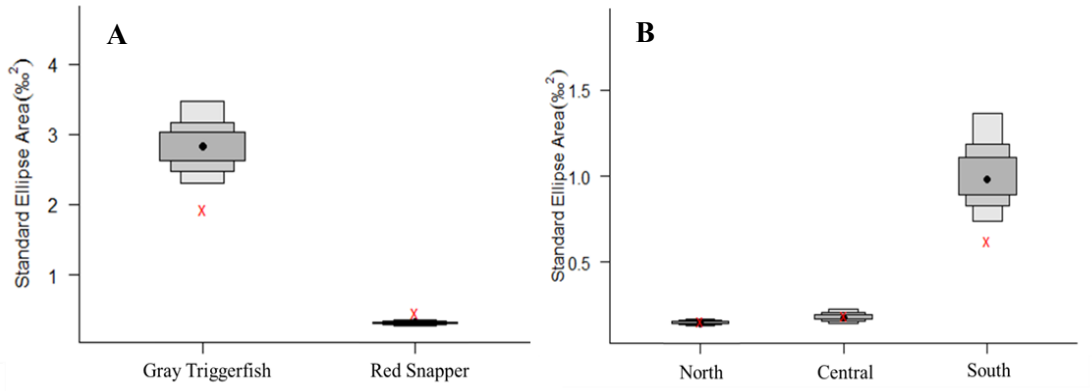

Figure A.5: Density plots representing Bayesian credibles for the standard ellipse area (SEA) based on $\delta^{13}C$ and $\delta^{15}N$ for Gray Triggerfish (n = 89), and Red Snapper (n = 182) (**A**) and the north (n = 203), central (n = 83), and south (n = 41) regions (**B**). Black points represent the mean, while gray boxes represent 50, 75, and 95 % credible intervals. Red x's represent the SEA corrected for sample size (SEA_c).

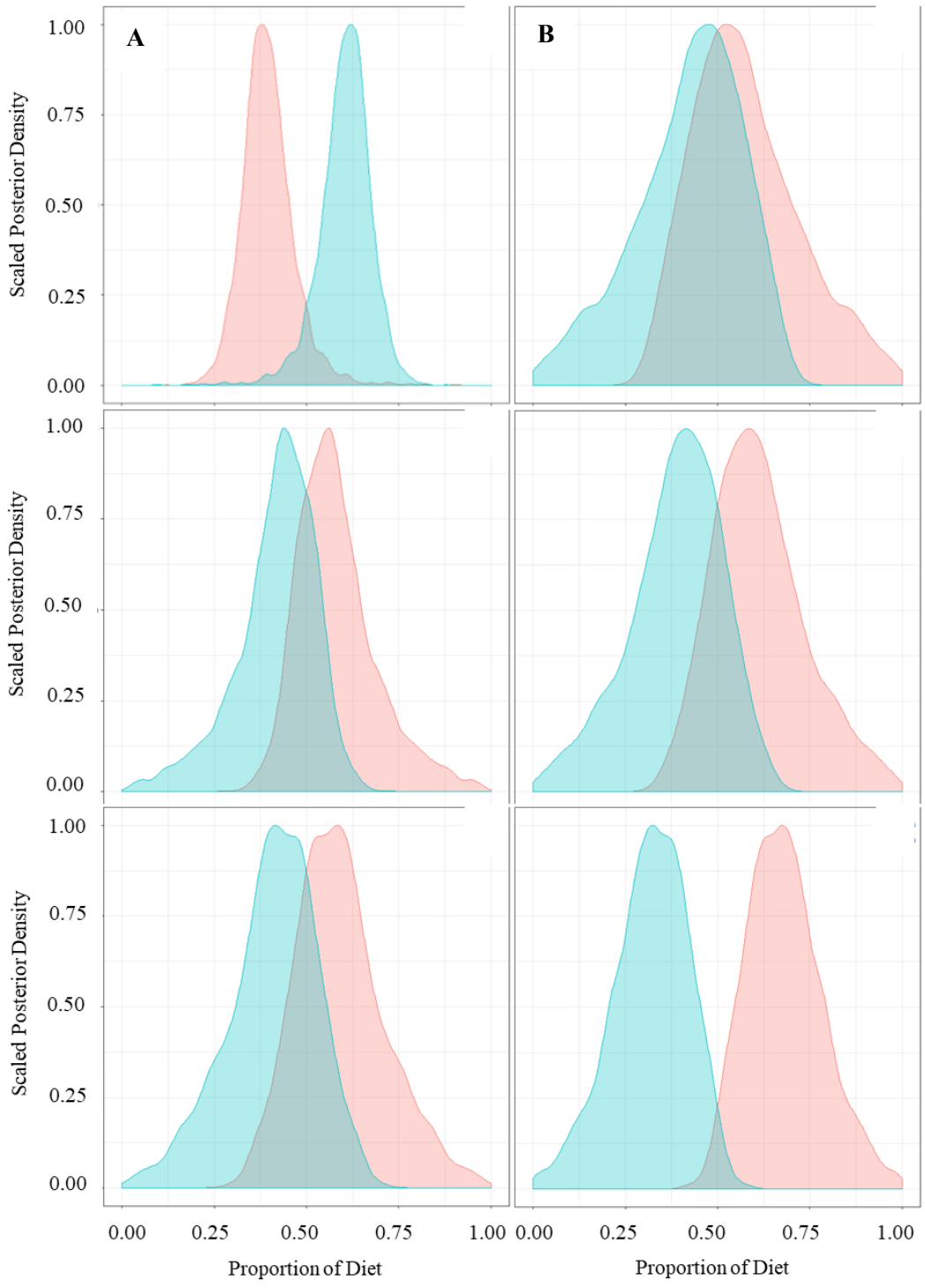

Figure A.6: Pelagic (POM, blue) and benthic (BMA, red) source contribution estimates for (**A**) Gray Triggerfish and (**B**) Red Snapper. Plots depict contributions for juvenile [Gray Triggerfish (n = 12), Red Snapper (n = 53)], sub-adult [Gray Triggerfish (n = 44), Red Snapper (n = 92)], and adult [Gray Triggerfish (n = 33), Red Snapper (n = 37)] fish from top to bottom, respectively.