Feeding ecology of three coastal shark species in the northwest Gulf of Mexico

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ABSTRACT: The feeding ecology of 3 coastal shark species — Atlantic sharpnose *Rhizoprionodon terraenovae*, bonnethead *Sphyrna tiburo*, and blacktip *Carcharhinus limbatus* shark — was examined in the northwest Gulf of Mexico (GOM). A total of 601 sharks (305 Atlantic sharpnose, 239 bonnethead, and 57 blacktip) were collected over 2 yr from recreational anglers in Galveston, TX. All individuals had stomach contents examined and a subset (50 Atlantic sharpnose, 50 bonnethead, and 36 blacktip sharks) was analyzed for stable isotopes (carbon, nitrogen, and sulfur) in muscle tissue, revealing short-term and long-term feeding strategies. Both blacktip and Atlantic sharpnose shark stomach contents consisted of teleost fishes with percent index of relative importance (%IRI) of 98.95 and 91.16, respectively, whereas bonnethead diets were dominated by crustaceans (%IRI = 87.20). Stable isotope analysis revealed bonnetheads had higher mean carbon ($\delta^{13}C$) and lower sulfur ($\delta^{34}S$) values, indicating inshore feeding and a preference for benthic invertebrates, respectively. Atlantic sharpnose and blacktip sharks were shown to feed on similar prey using stomach content analysis, yet Atlantic sharpnose sharks had a broader diet, including cephalopods and crustaceans in addition to teleost fishes. Differences were further established using nitrogen ($\delta^{15}N$) values, which were significantly lower for Atlantic sharpnose than blacktip sharks. Collectively, stomach contents and stable isotope analyses supported different feeding strategies of 3 common shark species. $\delta^{34}S$ appeared to serve as a natural tracer, distinguishing benthic versus pelagic feeding patterns in elasmobranchs. This study provides important ecosystem-based feeding information of upper trophic-level predators in coastal waters of the northwestern GOM.

KEY WORDS: Feeding ecology · Stable isotopes · Stomach contents · Gulf of Mexico

INTRODUCTION

Coastal ecosystems are characterized by high primary productivity (Nixon et al. 1986) and high faunal diversity (Ross 1986), which support broad ecological niches. Coastal bays within the northwestern Gulf of Mexico (GOM) fit this characterization, with high levels of nutrient input from the Mississippi River, and other rivers, driving productive coastal ecosystems. The northwest GOM is also a system in flux, with increasingly high levels of disturbance due to global warming, including habitat destruction and hypoxia, leading to periodic fluctuations in biodiver-sity (Rabalais et al. 2009). These varied modes of disturbance can affect the abundance of upper trophic-level predators such as sharks directly and through movement and density of their prey base (Heupel & Hueter 2002, Torres et al. 2006). One of the ways to understand the effects of environmental change on sharks is by analyzing regionally specific dietary trends, allowing estimation of potential changes in ecosystem structure.

Sharks within the Order Carcharhiniformes are among the most common species in coastal waters of the GOM (Burgess et al. 2005, Drymon et al. 2010, Bethea et al. 2015). Among the most abundant of

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these are the Atlantic sharpnose *Rhizoprionodon terraenovae*, bonnethead *Sphyrna tiburo*, and blacktip *Carcharhinus limbatus* sharks (Bethea et al. 2015). All 3 of these species are abundant along the Texas coast, but vary seasonally in their distributions (Froeschke et al. 2010). While distribution and abundance data for Atlantic sharpnose, bonnethead, and blacktip sharks in the northwest GOM exist, little information is available regarding their feeding habits, which is essential to understanding how their presence affects ecosystem structure and functioning. Elasmobranchs have been shown to have latitudinal and longitudinal dietary shifts that are important to understand when creating accurate ecosystem models (Bethea et al. 2007, Drymon et al. 2012).

While similar in range, these species differ slightly with respect to assumed feeding patterns in other regions (Castro 1996, Cortés et al. 1996, Bethea et al. 2006). East of the Mississippi River, blacktip sharks are known piscivores, targeting teleost prey within the families Sciaenidae and Clupeidae, along with other baitfish and larger teleost fishes as they mature (Branstetter 1987, Castro 1996, Barry et al. 2008). Atlantic sharpnose sharks are more opportunistic, focusing on crustaceans (e.g. shrimp) when they are juveniles and teleost fishes, cephalopods, and portunid crabs as they mature (Bethea et al. 2006, Drymon et al. 2012). Bonnetheads are primarily benthic feeders, targeting stomatopods, shrimp, portunid crabs, and cephalopods as juveniles, then becoming more specialized on blue crabs *Callinectes sapidus* as adults (Cortés et al. 1996, Bethea et al. 2007).

Examination of diet and foraging patterns where there is known species mixing can aid in understanding resource partitioning and trophic structure (Papastamatiou et al. 2006, Kinney et al. 2011). Pairing dietary information with stable isotope analysis provides a comprehensive assessment of feeding strategies on a small spatial scale (Post 2002). This combination of techniques offers useful information about short- and long-term feeding patterns, respectively (Wells et al. 2008, Kinney et al. 2011). Stomach contents highlight feeding habits on a short temporal scale (hours to days) (Hynes 1950, Hyslop 1980, Cortés 1997), while stable isotope analysis using carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) can provide feeding information on temporal scales of weeks, months, and years, depending upon species-specific and tissue-specific turnover rates (DeNiro & Epstein 1978, Post 2002, Hussey et al. 2012). $\delta^{13}C$ ratios are widely used to identify the source(s) of primary production and $\delta^{15}N$ can determine trophic levels (DeNiro & Epstein 1978, Post 2002, Hussey et al.

2012). In addition, $\delta^{34}S$ has been shown to contrast benthic versus pelagic foraging strategies in teleost fishes (Peterson & Fry 1987, Thomas & Cahoon 1993, Wells et al. 2008). $\delta^{34}S$ values tend to be lower in benthic zones due to the increased percentage of sulfides in the sediment, but higher in the water column where an increase in sulfates occurs (Peterson 1999, Fry et al. 2008, Kiyashkoa et al. 2011). Collectively, these 3 natural tracers, combined with stomach content analysis, have not been used in elasmobranch feeding studies to describe overall trophic and ecosystem structure within the marine food web.

The objective of this study was to examine the feeding strategies of 3 coastal shark species in the northwest GOM. Factors of sex, year, month, location, and ontogeny were used when identifying intraspecific trends in diet. We used stomach content analysis to quantify dietary breadth and to examine the importance of individual prey items in the diet of each shark species. In addition, we used bulk stable isotope ratios of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ to examine food web structure, to elucidate feeding ecology of the 3 species, and compare individual dietary preferences. Ultimately, we aim to better understand the dietary niche of each species and use these data for ecological models for ecosystem-based fisheries management.

MATERIALS AND METHODS

Sample collection

This study draws from a dataset of opportunistic samples collected from April through October of 2013 and 2014 from Galveston, Texas. The majority of samples (n = 593) were collected dockside from recreational anglers via hook and line, along with specimens collected from the Texas Parks and Wildlife Department bottom longline survey (n = 8). Sample location and information regarding bait type used was assessed through personal communication with anglers. All sharks used for the study were taken during day trips throughout waters surrounding Galveston, which minimized likelihood for variations in the base of the food web. Each shark was sexed and measured along a straight line to the nearest centimeter to obtain total length (TL), fork length (FL), and precaudal length (PCL). Stomachs were removed from individuals at the dock and sealed via zip tie at the esophageal end of the stomach and the anterior end of the scroll valve so that no contents were lost. Epaxial muscle tissue was removed from each specimen anterior to the primary dorsal fin for

stable isotope analysis. If the dorsal fin location could not be assessed after processing, muscle tissue was removed from the dorsal portion of the vertebral column.

Stomach content and stable isotope procedures

Stomachs were preserved via a 48 h fixing process in 10% formalin and then moved to a solution of 70% ethyl alcohol for longer-term storage. Each stomach was measured for full wet weight (g), opened, and separated with a series of 3 metal mesh sieves sized 1.27 cm, 1400 μm, and 500 μm. All contents including otolith, bone and carapace found within the stomachs were identified to the lowest possible taxon. Once identified, contents were sorted and weighed to the nearest 0.1 g. If bait was found that was previously identified through angler interviews, it was weighed and removed from subsequent analysis.

Muscle tissue samples were immediately catalogued and frozen at −20°C upon return to the lab. During processing, tissue samples were dried at 60°C for 48 h in a Heratherm OGS180 drying oven (ThermoScientific) then lipid was extracted via the Dionex Accelerated Solvent Extractor 35. The extraction process used 34 ml cells packed with layered tissue samples separated by 30 mm Whatman filter papers, and ran in cycles of 5 min saturations with petroleum ether at 100°C and 1500 psi (105.5 kg cm^{-2}) in order to reach thermal equilibrium, followed by a flush with fresh solvent. This procedure was repeated 3 times per cell to ensure the removal of lipids. Following lipid extraction, tissue was homogenized via a Wig-L-Bug® grinding mill and further dried at 60°C for 24 h to remove any additional solvent. Once dry, the tissue was encapsulated using 5 × 9 mm tin capsules, placed in a 96 plate well, and shipped for analysis. Analysis of the stable isotopes δ^{13}C and δ^{15}N was performed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (IRMS) (Sercon), and δ^{34}S analysis was done using an Elementar vario ISOTOPE cube interfaced to a 20-22 IRMS (Sercon). Heavy isotopes were compared to laboratory standards; carbon was compared via Vienna PeeDee Belemnite, nitrogen was compared via atmospheric N$_2$, and sulfur was compared via Vienna Canon Diablo Trilobite. All analysis was done through the Stable Isotope Facility at the University of California at Davis. Stable isotope data were presented in delta notation, $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is the heavy isotope, R_{sample} is the ratio of heavy to light isotope in the sample, and $R_{standard}$ is the ratio of heavy to light isotope in the reference standard. The need for lipid extraction was confirmed using replicate samples of extracted and non-extracted tissue. For each species, 10 samples of muscle tissue were selected for comparison. Half of each sample selected underwent lipid extraction and the remaining half of the sample was left unaltered. The samples of extracted and non-extracted tissue were compared via paired Student's t-test. Significant differences (α ≤ 0.05) were detected between mean δ^{13}C and δ^{15}N stable isotope ratios in both blacktip and Atlantic sharpnose sharks, while δ^{34}S, along with all stable isotope ratios in bonnetheads, had no significant differences between extracted and non-extracted tissue. Post-extraction tissue was raised to the threshold C:N ratio described in Hussey et al. (2011) of 3.0, which is closest to pure protein and ideal when conducting stable isotope analysis. To ensure homogeneity among all tissues, all samples were lipidextracted to remove effects of high lipid concentration, as well as soluble urea, on isotopic ratios.

Data analysis

Feeding patterns were investigated according to interspecific differences. In addition to differences among species, intraspecific differences were identified using sex, year, ontogeny (length and maturity), and month as factors. Shark species were separated by maturity for intraspecific analysis, based on length at 50% maturity (LF50) measurements for each species (Baremore & Passerotti 2013, Hoffmayer et al. 2013, Frazier et al. 2014); however, owing to a low comparable sample size between mature and immature for all species, samples were placed into 10 cm size bins using FL for interspecific analysis. Analysis regarding stomach contents was done by organizing the taxonomic groups found within the stomachs into higher categories; highest level taxa were achieved at the subphylum and infraclass levels (Teleostei, Crustacea, and Cephalopoda), while less common taxa were grouped into Other (Echinodermata, Bivalvia, Gastropoda, and various algae). For further classification detail among groups, Teleostei and Crustacea were broken down using prey groupings similar to the ones described in Bethea et al. (2004) and Bethea et al. (2007). Groupings included epibenthic teleost, pelagic teleost, penaeid shrimp, brachyurans, other crustaceans, and cephalopods. Unidentified material from Teleostei and Crustacea were removed from this analysis. A percent index of

relative importance (%IRI) was computed for prey items using percent weight (%W), percent numerical quantity (%N), and percent frequency of occurrence (%O) (Pinkas et al. 1971, Cortés 1997):

$$IRI = (\%N + \%W) \times \%O \tag{1}$$

$$\%IRI = \left(\frac{IRI_{prey}}{IRI_{total}} \right) \times 100 \tag{2}$$

For analysis using stomach contents, %W was used to calculate differences among species, as it is a metric that is frequently used to quantify nutritional contribution (Rooker 1995). Stomach contents by %W were analyzed using ANOSIM with a Bray-Curtis similarity matrix, and additional information to identify the most important prey items was provided using SIMPER analysis. Both ANOSIM and SIMPER non-parametric statistical techniques were carried out using PRIMER v.7 (Clarke & Gorley 2015). Stomachs containing contents with negligible weight, but identifiable contents, were excluded from %W calculations, yet included on %IRI analysis. Further analysis was conducted using the Shannon-Wiener diversity index (H'), incorporating both species evenness index (J') and species richness (S), to quantify the diversity of the diet of each species:

$$H' = \sum_{i=1}^{S} p_i \ln p_i \tag{3}$$

where p_i is the proportional abundance of species i:

$$p_i = \frac{n_i}{N} \tag{4}$$

H max = ln S and J' is therefore H' divided by H_max or (ln S):

$$J' = \frac{H'}{H_{max}} \tag{5}$$

Along with prey diversity, trophic level was estimated using stomach contents and standardized prey item trophic positions were estimated similar to Cortés (1999). Taxonomic richness was also assessed via cumulative prey curve (CPC) to assess if the breadth of each species diet had been fully described (Ferry & Cailliet 1996).

MANOVA models were applied to incorporate $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ to assess differences among species. ANOVA models were then used to compare differences among species using individual stable isotope values. Simple linear regressions were used to determine any length effects correlated with $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. When length was determined to have a significant effect, it was selected as a covariate and incorporated into ANCOVA models, which were used for intraspecific analyses using ANOVA models. Statistical significance was assessed at $\alpha \leq 0.05$ and all parametric tests were analyzed using SYSTAT (Cranes Software International).

Quadratic discriminant function analysis (QDFA) was used to test the ability of %W of major taxonomic groups and stable isotope ratios of shark tissue to distinguish uniqueness of their feeding strategies based upon individual species. Jackknife cross-validated classifications were used to quantify classification success to respective species based upon dietary contribution. QDFA models were based on residuals of %W of major taxonomic groups (Teleostei, Crustacea, Cephalopoda, and Other) and $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. Classification success has an inverse relationship to levels of dietary overlap: high levels of overlap are reflected in low percent classification success, while low levels of overlap are reflected in high percent classification success among the 3 species.

RESULTS

A total of 601 (n = 305 Atlantic sharpnose, n = 239 bonnethead, and n = 57 blacktip sharks) stomachs were analyzed in this study. Of those, 83.3% (n = 254) Atlantic sharpnose, 92.5% (n = 221) bonnethead, and 61.4% (n = 35) blacktip shark stomachs contained identifiable contents and were used for statistical analysis. Along with stomachs analyzed, 136 (n = 50 Atlantic sharpnose, n = 50 bonnethead, and n = 36 blacktip shark) tissue samples were used for stable isotope analysis. Size ranges and sex ratios varied for collected samples of each species: Atlantic sharpnose shark 51.3 to 89.5 cm FL (48 females, [mean ± SE] FL = 80.7 ± 1.0 cm; 257 males, FL = 77.4 ± 0.4), bonnethead 49 to 102 cm FL (166 females, FL = 82.4 ± 0.7 cm; 73 males, FL = 77.2 ± 0.7 cm), and blacktip shark 52.7 to 143.7 FL (31 females, FL = 108.1 ± 3.0 cm; 26 males, FL 94.5 ± 3.5 cm) (Fig. 1).

Stomach contents

Among the 3 species, 54 individual taxonomic groups were identified through stomach content analysis, with 23 taxa being identified to the species level. Samples from Atlantic sharpnose sharks contained 37 taxonomic groups, bonnetheads contained 23 taxonomic groups, and blacktip sharks contained 14 taxonomic groups. Both Atlantic sharpnose sharks

and bonnetheads had CPCs reaching an asymptote, while blacktip sharks did not, indicating further sampling is needed to fully describe the diet of this species in this region. Trophic position, estimated using
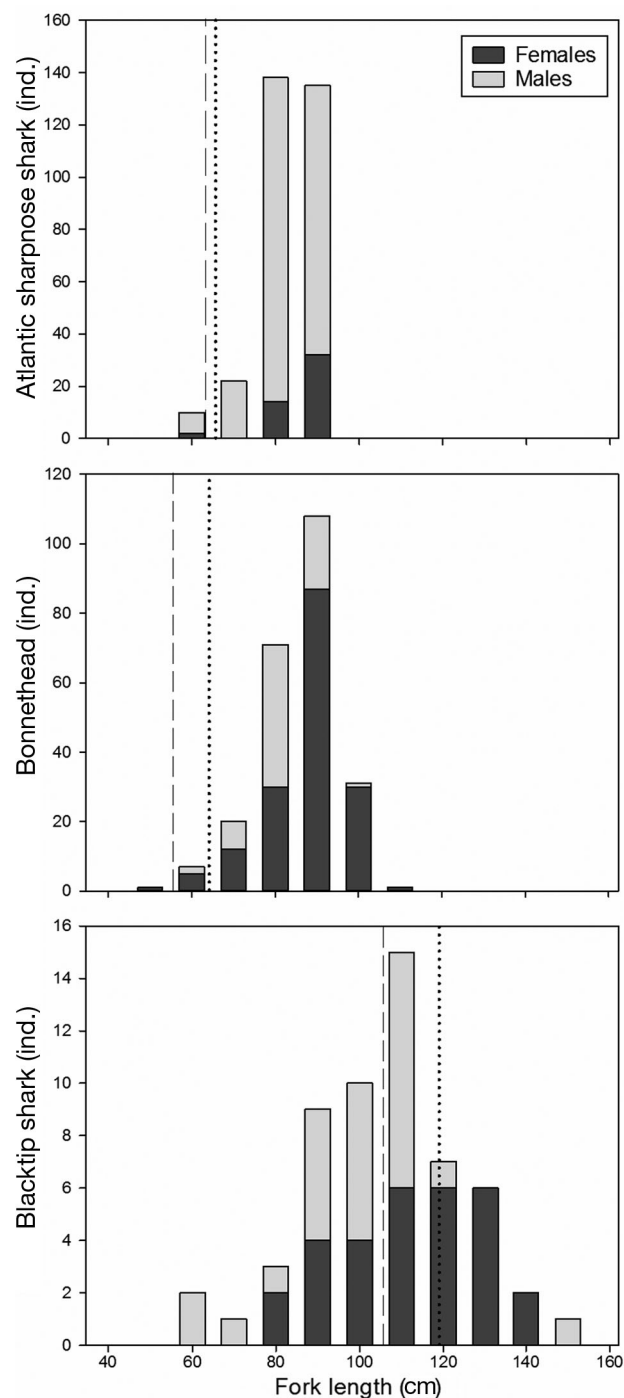

Fig. 1. Size distributions of Atlantic sharpnose (n = 305), bonnethead (n = 239), and blacktip (n = 57) sharks collected in 2013 and 2014 from Galveston, Texas. Lines indicating median ages of maturity (dashed lines: male; dotted lines: female) are noted on the histograms based on length at 50% maturity (LF50) measurements for each species

stomach contents, for blacktip sharks (4.22) was similar to what was found by Cortés (1999) off of the western Atlantic Ocean. However, Atlantic sharpnose sharks (4.20) and bonnetheads (3.40) were found to be closer than estimated previously in the GOM, and values were higher than those estimated from the western Atlantic (Delorenzo et al. 2015). Dietary taxonomic diversity was determined using H', supporting that Atlantic sharpnose sharks had the highest S (Atlantic sharpnose shark = 37, bonnethead = 23, blacktip shark = 14) and bonnetheads had the highest J' (Atlantic sharpnose shark = 0.52, bonnethead = 0.62, blacktip shark = 0.32) and overall H' (Atlantic sharpnose shark = 1.99, bonnethead = 2.39, blacktip shark = 1.22).

Stomach contents from both blacktip and Atlantic sharpnose sharks (Tables S1 & S2, respectively, in the Supplement at www.int-res.com/articles/suppl/m550p163_supp.pdf) consisted primarily of unidentified teleosts, (%IRI = 91.16 and 98.95, respectively). Primary prey categories for Atlantic sharpnose sharks included unidentified Teleostei (87.40%IRI), Penaeidae (3.56%IRI), and Teuthoidea (2.92%IRI). Within identified Teleostei, the largest contributing fish taxon to the diet of Atlantic sharpnose sharks was family Sciaenidae (1.84%IRI). Blacktip sharks had primary prey categories of unidentified Teleostei (88.52%IRI) and Atlantic croaker *Micropogonias undulatus* (7.46%IRI), while additional overall non-teleost prey categories (Crustacea, Cephalopoda, and Other) summed to 1.15%IRI. Diet of bonnetheads (Table S3) consisted primarily of crustaceans (87.20%IRI), with the top 3 contributors as unidentified Brachyuran (48.91%IRI), *Callinectes sapidus* (18.06%IRI), and *C. similis* (3.32%IRI) (Fig. 2).
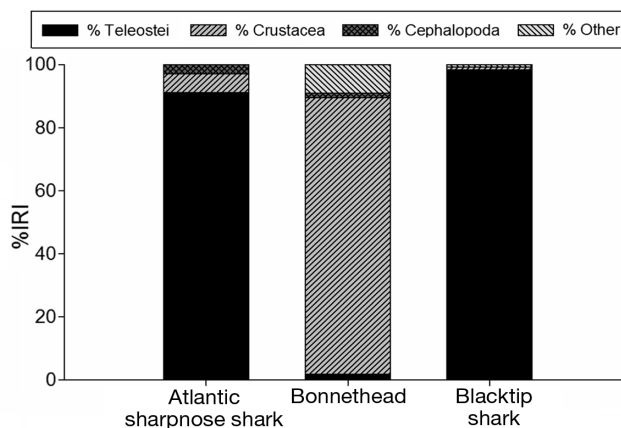

Fig. 2. %IRI contributions of each of the dietary categories, using major overall taxonomic groups for Atlantic sharpnose (n = 254), bonnethead (n = 221), and blacktip sharks (n = 35)

ANOSIM was used to compare stomach contents (%W) for 3 species of shark across the following categories: Teleostei, Crustacea, Cephalopoda, and Other. ANOSIM for among species analysis was significantly different (global R = 0.501, p ≤ 0.05). Pairwise analysis within ANOSIM revealed significant differences between Atlantic sharpnose sharks and bonnetheads (global R = 0.534, p ≤ 0.05) as well as blacktip sharks and bonnetheads (global R = 0.892, p ≤ 0.05), while no difference was denoted between Atlantic sharpnose and blacktip sharks (global R = −0.186, p > 0.05). SIMPER analysis showed %W of Crustacea was the most important contributor driving diet differences between bonnetheads and blacktip sharks (93.27 average dissimilarity), and bonnetheads and Atlantic sharpnose sharks (75.52 average dissimilarity), with highest values associated with bonnetheads. High %W of Teleostei combined with low %W of Crustacea were noted for blacktip sharks, while higher %W of Cephalopoda was also shown to differ in Atlantic sharpnose shark diet relative to blacktip sharks (32.81 average dissimilarity).

To infer further relationships, and due to low applicable samples sizes of various taxonomic groups, ANOSIM was run among species using prey groupings epibenthic teleost, pelagic teleost, brachyuran, penaeid shrimp, other crustaceans, and cephalopods. Using these groupings, significant differences were found among species (global R = 0.576, p ≤ 0.05). Pairwise analysis within ANOSIM revealed significant differences between Atlantic sharpnose sharks and bonnetheads (global R = 0.573, p ≤ 0.05), and blacktip sharks and bonnetheads (global R = 0.903, p ≤ 0.05), while no difference was denoted between Atlantic sharpnose and blacktip sharks (global R = −0.011, p > 0.05). SIMPER analysis showed %W of brachyurans in bonnetheads and %W of epibenthic and pelagic teleosts in blacktip sharks (99.07 average dissimilarity) along with Atlantic sharpnose sharks

(75.52 average dissimilarity) being the largest difference among the 3 species. High %W of epibenthic teleosts combined with low %W of penaeid shrimp were noted differences between blacktip and Atlantic sharpnose shark stomach contents. ANOSIM was also run using sex, month, year, length, and maturity level as intraspecific factors for each of the 3 species. No intraspecific factor was found to be significant using stomach content data.

Stable isotope analysis

Analysis with MANOVA for among species comparisons using all stable isotope ratios (δ^{13}C, δ^{15}N, and δ^{34}S) indicated significant differences among species ($F = 29.697$, p ≤ 0.05). Individual ANOVAs were then conducted using individual stable isotope ratios among species. δ^{13}C was significantly different among species ($F = 3.119$, p ≤ 0.05), with highest values in bonnetheads (−16.89 ± 0.05‰, mean ± SE), followed by blacktip sharks (−16.94 ± 0.04‰), and Atlantic sharpnose sharks (−17.03 ± 0.03‰). δ^{15}N was also significantly different across species ($F = 9.453$, p ≤ 0.05) with highest values for blacktip sharks (16.43 ± 0.09‰), followed by Atlantic sharpnose sharks (16.04 ± 0.08‰), and lastly bonnetheads (15.91 ± 0.08‰). δ^{34}S was significantly different among species ($F = 8.840$, p ≤ 0.05), with highest values in blacktip sharks (16.79 ± 0.14‰), followed by Atlantic sharpnose sharks (16.70 ± 0.16‰), and bonnetheads (15.94 ± 0.16‰) (Table 1, Fig. 3).

Intraspecific analysis was performed using ANOVA with month, sex, maturity, and year as factors for each of the stable isotope ratios. δ^{13}C was higher for mature bonnetheads ($F = 13.347$, p ≤ 0.05) and blacktip sharks ($F = 5.430$, p ≤ 0.05), as well as blacktip sharks collected in 2013 relative to 2014 ($F = 5.271$, p ≤ 0.05). δ^{15}N was higher for female, relative

Table 1. ANOVA results for stable isotope ratios among species. **Bold**: significantly different at p ≤ 0.05

Test	R^2	F	p	Pairwise Tukey's HSD	p
δ^{13}C	0.047	3.119	**0.047**	Atlantic sharpnose shark vs. bonnethead shark	**0.036**
				Atlantic sharpnose shark vs. blacktip shark	0.325
				Blacktip shark vs. bonnethead shark	0.682
δ^{15}N	0.124	9.453	**<0.001**	Atlantic sharpnose shark vs. bonnethead shark	0.440
				Atlantic sharpnose shark vs. blacktip shark	**0.005**
				Blacktip shark vs. bonnethead shark	**<0.001**
δ^{34}S	0.117	8.840	**<0.001**	Atlantic sharpnose shark vs. bonnethead shark	**0.001**
				Atlantic sharpnose shark vs. blacktip shark	0.913
				Blacktip shark vs. bonnethead shark	**0.001**

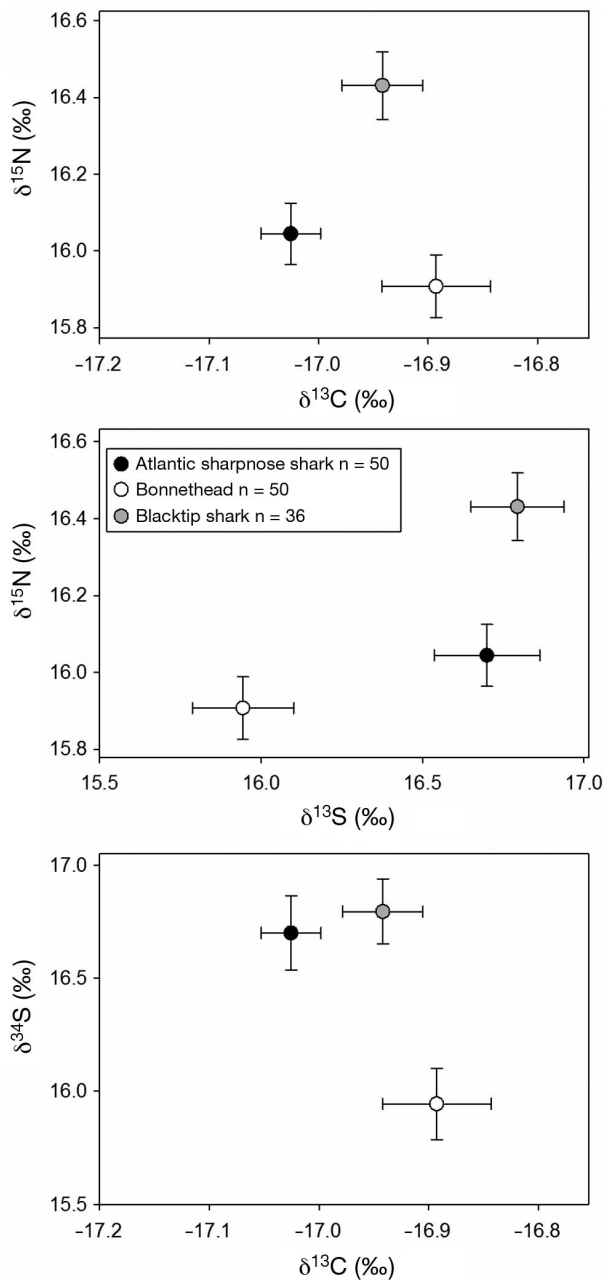Fig. 3. Biplots of mean (±SE) stable isotope ratios for Atlantic sharpnose, bonnethead, and blacktip shark species using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$

Regression analysis was run for each stable isotope on each species and compared to FL to examine ontogenetic patterns. Blacktip shark length had a significant positive linear relationship with $\delta^{13}C$ (R^2 = 0.114, p = < 0.05) and $\delta^{15}N$ (R^2 = 0.128, p = < 0.05), and bonnethead length had a significant negative linear relationship with $\delta^{34}S$ (R^2 = 0.107, p = < 0.05), while Atlantic sharpnose sharks showed no significant linear relationships (Fig. 4).

Jackknife reclassification success using QDFA was calculated for each species to estimate dietary overlap. Reclassification success was highest with %W combined with all 3 stable isotope ratios for bonnetheads (93%) as well as blacktip sharks (76%), and lowest for Atlantic sharpnose sharks (24%) due to higher overlap. Reclassification using %W alone was most useful in identifying specialization of feeding within the dataset (92% bonnethead, 96% blacktip shark, and 17% Atlantic sharpnose shark), while reclassification using only stable isotope ratios yielded less accurate yet more evenly distributed classification success (58% bonnethead, 61% blacktip shark, and 38% Atlantic sharpnose shark).

DISCUSSION

Both stomach content and stable isotope analyses support different feeding patterns for 3 common shark species in the northwest GOM. Several studies have shown an overlap of range for these 3 species in the GOM (Drymon et al. 2010, Bethea et al. 2015) and along the coast of Texas (Froeschke et al. 2010). However, until now there have been few observations regarding their compared feeding strategies in the northwest GOM. Bonnetheads were found to be most different, with the vast majority of the diet consisting of benthic invertebrates. Blacktip and Atlantic sharpnose sharks both had diets consisting mostly of teleost fishes, primarily from the family Sciaenidae. Fishes that feed throughout the water column contain a higher amount of sulfates (SO_4) and higher respective $\delta^{34}S$ values than organisms that specialize on benthic prey such as crustaceans and other benthic invertebrates (Peterson & Fry 1987), and these patterns were clearly demonstrated by bonnetheads with lower $\delta^{34}S$ values and a diet primarily of crustaceans (87 %IRI). In contrast, higher $\delta^{34}S$ values were reflective in both blacktip and Atlantic sharpnose sharks, which both had teleost-dominated diets (98 and 91 %IRI, respectively). Blacktip sharks were more specialized feeders, when compared to Atlantic sharpnose sharks, consuming almost exclusively

to male Atlantic sharpnose sharks (F = 39.214, p ≤ 0.05); however, no sex-specific differences were observed for the other 2 species. $\delta^{34}S$ was significantly higher for all species in 2014 relative to 2013: Atlantic sharpnose sharks (F = 14.155, p ≤ 0.05), bonnetheads (F = 11.927, p ≤ 0.05), and blacktip sharks (F = 5.906, p ≤ 0.05). $\delta^{34}S$ was also higher in immature bonnetheads relative to mature for both years (F = 9.340, p ≤ 0.05) (Table 2).

Table 2. Mean (±SE) differences of stable isotope ratios among maturity (mature/immature), year (2013/2014), and sex (male/female). **Bold**: significantly different using ANOVA at p ≤ 0.05

Dependent variable	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
Atlantic sharpnose shark			
Maturity (mature/immature)	−17.02 ± 0.03/	16.05 ± 0.09/	16.68 ± 0.19/
	−17.04 ± 0.06	16.01 ± 0.16	16.79 ± 0.36
Year (2013/2014)	−17.07 ± 0.03/	15.94 ± 0.12/	**16.15 ± 0.26/**
	−16.98 ± 0.04	16.15 ± 0.11	**17.25 ± 0.12**
Sex (male/female)	−17.04 ± 0.03/	**16.25 ± 0.07/**	16.77 ± 0.16/
	−16.99 ± 0.06	**15.33 ± 0.10**	16.46 ± 0.48
Bonnethead			
Maturity (mature/immature)	**−16.83 ± 0.04/**	15.94 ± 0.07/	**15.78 ± 0.16/**
	−17.33 ± 0.19	15.69 ± 0.47	**17.15 ± 0.27**
Year (2013/2014)	−16.84 ± 0.07/	15.90 ± 0.11/	**15.45 ± 0.20/**
	−16.95 ± 0.07	15.91 ± 0.12	**16.43 ± 0.20**
Sex (male/female)	−16.81 ± 0.04/	16.06 ± 0.08/	15.74 ± 0.24/
	−16.93 ± 0.07	15.83 ± 0.11	16.13 ± 0.20
Blacktip shark			
Maturity (mature/immature)	**−16.83 ± 0.07/**	16.67 ± 0.21/	16.71 ± 0.21/
	−17.00 ± 0.04	16.31 ± 0.08	16.84 ± 0.19
Year (2013/2014)	**−17.06 ± 0.05/**	16.64 ± 0.20/	**16.30 ± 0.18/**
	−16.89 ± 0.04	16.34 ± 0.09	**17.01 ± 0.18**
Sex (male/female)	−17.00 ± 0.05/	16.31 ± 0.08/	16.68 ± 0.24/
	−16.89 ± 0.06	16.54 ± 0.15	16.90 ± 0.17

teleost fishes with corresponding higher $\delta^{15}N$ values reflective of a diet that consisted of higher trophic-level prey items. Atlantic sharpnose sharks were found to feed more generally, with stomachs containing a mixture of teleost fishes along with crustaceans and cephalopods. Atlantic sharpnose sharks also had corresponding lower $\delta^{15}N$ values, consistent with a diet of lower trophic-level teleost prey items and increased contributions from other lower trophic-level taxa. Bonnethead samples contained the lowest $\delta^{15}N$ values, which reflected feeding on the lowest trophic level of the 3 species. All 3 species had overlapping $\delta^{13}C$ values; however, bonnetheads had significantly higher mean values, suggesting a more inshore feeding strategy versus an offshore feeding strategy shown by the lower mean $\delta^{13}C$ values of the other 2 species (Hussey et al. 2012).

The piscivorous feeding strategy of blacktip sharks found in the northwest GOM is similar to other studies throughout the GOM. A full breadth of diet analysis was challenging due to the large proportion of empty stomachs in blacktip sharks (61% of stomachs), which has also been seen in previous studies (Hoffmayer & Parsons 2003, Barry et al. 2008). This proportion of empty stomachs is possibly due to the caveat of hook and line sampling. Hook and line sampling has the potential to attract active animals

on the search for food versus other more active gear types, which are less discriminatory towards animals with higher levels of satiation (Cortés 1997). The diet of blacktip sharks primarily consisted of teleost fishes, a majority of which were in the family Sciaenidae. The dominant fish species identified in the stomachs of blacktip sharks was Atlantic croaker *Micropogonias undulatus*. Atlantic croaker was found to be far more abundant in blacktip shark diets relative to gulf menhaden *Brevoortia patronus*, which dominated in other studies (Hoffmayer & Parsons 2003, Bethea et al. 2004, Barry et al. 2008). Blacktip sharks have also been shown to have high levels of sympatry with menhaden, being a high percentage of bycatch in the menhaden commercial fishery (de Silva et al. 2001). Both species are abundant in Galveston Bay (Rozas & Zimmerman 2000) and along the nearshore waters of the Texas coast (Lewis et al. 2007). Gulf menhaden and the Atlantic menhaden *B. tyrannus* have been shown to be the primary prey for blacktip sharks from studies in Louisiana, Mississippi, and Florida (Hoffmayer & Parsons 2003, Bethea et al. 2004, Barry et al. 2008), yet were found in lower abundance when compared to Atlantic croaker in blacktip shark diets. The GOM experienced a decline of over 50% in total catch of menhaden from 2009 to 2013, while for those same years, total catch of Atlantic croaker in the GOM stayed relatively constant (4% increase) (NOAA Fisheries 2015). Annual fluctuations in abundance may contribute to the low number of gulf menhaden found in the diets of blacktip sharks in our study along with the aforementioned lack of samples.

Ontogenetic diet shifts were detected using stable isotope ratios for blacktip shark. Both $\delta^{13}C$ and $\delta^{15}N$ were found to have positive relationships with length, confirming shifts in the diets of blacktip sharks with increasing age. Ontogenetic diet shifts have been identified in teleost fishes and chondrichthyans (Fry et al. 1999, Albo-Puigserver et al. 2015) using both $\delta^{13}C$ and $\delta^{15}N$. Increasing $\delta^{15}N$ is indicative of predation on larger prey as well as increased trophic level with age, which corresponds to known dietary information for blacktip sharks (Castro 1996, Hoffmayer & Parsons 2003, Barry et al. 2008, Bornatowski et al.
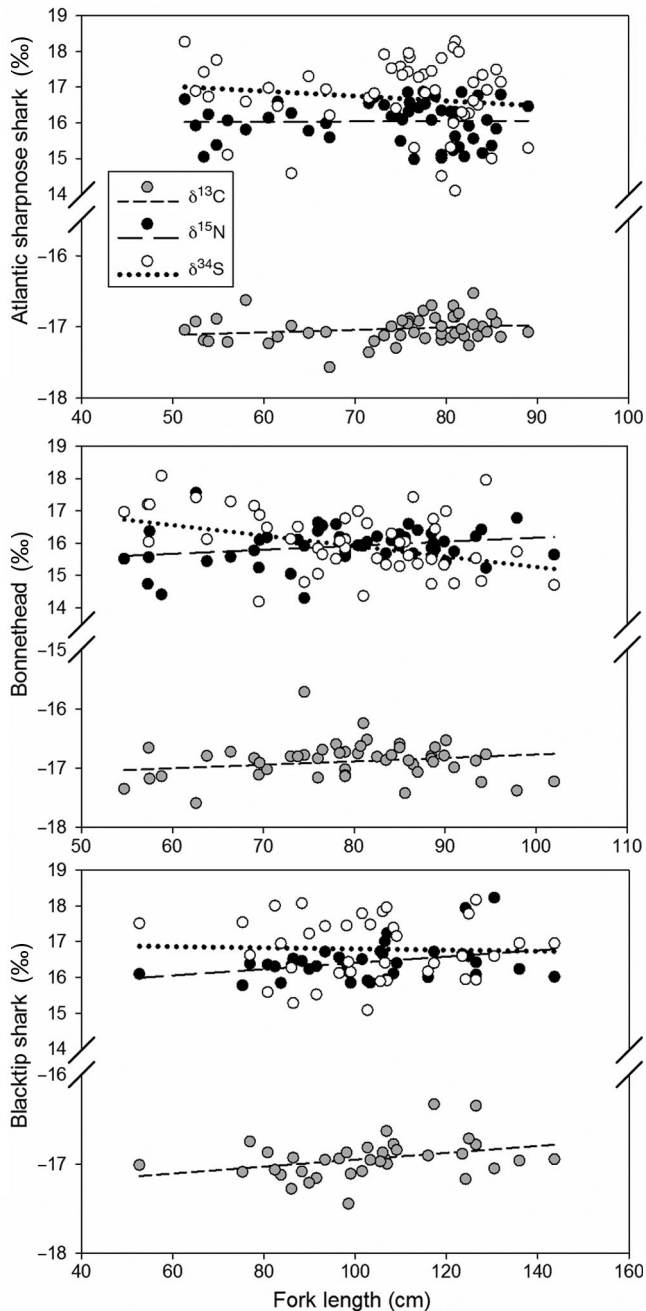
Fig. 4. Simple linear regression lines for Atlantic sharpnose, bonnethead, and blacktip sharks, comparing fork length (FL) to stable isotope values $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$

2014). The overall change in $\delta^{13}C$ indicates an increase in movement and expansion of home range as ontogenetic dietary shifts occur. Dietary shifts resulting from movement offshore can account for up to a 4‰ in $\delta^{13}C$, which has been demonstrated through teleost fishes and elasmobranchs (Leakey et al. 2008, Hussey et al. 2011). Blacktip sharks have been shown to be highly migratory, with regular seasonal migra-

tions away from the coast as they age, which are driven primarily by seasonal changes in temperature in the GOM (Heupel & Simpfendorfer 2002, Hueter et al. 2005). These seasonal movements to maximize their ectothermic metabolisms (Papastamatiou & Lowe 2012) may explain the difference in source pathway, $\delta^{13}C$, as the sharks begin to migrate as they grow larger and mature.

Bonnetheads were found to have a very narrow dietary niche, with a diet dominated by the blue crab *Callinectes sapidus*. Blue crab has been shown in several studies throughout the GOM and the northwest Atlantic Ocean to be a primary item in the diet of bonnetheads (Cortés et al. 1996, Bethea et al. 2007). Our findings confirm a similar diet preference for blue crab with a focus on lesser blue crab *C. similis* and stomatopods. A significant amount of plant material, primarily benthic macroalgae, was found in 36% of the stomachs of bonnetheads, which was likely a result of incidental ingestion when pursuing benthic invertebrates. Cortés et al. (1996) found contributions from 3 species of sea grass (*Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*) in 56% of bonnethead stomachs in southwest Florida. Bethea et al. (2007) also found significant contributions from plant matter in the diets of bonnetheads, especially for young-of-the-year sharks. The primary vegetative matter found for our study area was strictly green (Chlorophyta) and brown algae (Phaeophyta), with no contributions from seagrasses or other angiosperms. This confirms the regionally related trends regarding vegetative matter ingestion, with primary vegetative matter consumed being algae, rather than seagrass, due to Galveston Bay's low amount of seagrass beds and high amount of benthic macroalgae (Pulich & White 1991).

Stable isotope analysis for bonnetheads mirrored the unique feeding strategies revealed through stomach content analysis. Analysis revealed significantly lower $\delta^{34}S$ and $\delta^{15}N$, indicating benthic invertebrate predation and lower trophic-level feeding. Ontogenetic diet shifts were detected for bonnetheads between $\delta^{34}S$ values and length. Previous studies of bonnetheads observed ontogenetic diet shifts with increasing specificity towards larger blue crab, and moving away from other smaller prey items. Bethea et al. (2007) and Cortés et al. (1996) found strong positive correlations between carapace length of ingested blue crabs and size of bonnetheads, confirming changes in prey preference with size. Our findings did not show any correlation for diet preference changing with size for bonnetheads; however, $\delta^{34}S$ showed a negative relationship with shark FL,

indicating an increase of specificity in benthic invertebrate consumption (Fry et al. 2008, Wells et al. 2008). Ontogenetic changes were also detected in $\delta^{13}C$ between immature and mature bonnetheads, which may also be linked to blue crabs. Blue crabs spawn over several months from April to November, primarily in June through August, with larger females having several batches of eggs per season (Dickinson et al. 2006, Graham et al. 2012). When spawning, females move into offshore waters of higher salinity when a corresponding pattern of older individuals are observed offshore (Dickinson et al. 2006). This movement of prey can potentially drive larger bonnetheads further from the coast, which is reflected in the decrease in $\delta^{13}C$ and confirmed using observed offshore seasonal movement patterns (Heupel et al. 2006, Ubeda et al. 2009, Driggers et al. 2014).

Atlantic sharpnose sharks were shown to be opportunistic predators, consuming a wide assortment of taxonomic groups including teleost fishes, crustaceans, and cephalopods. Atlantic sharpnose sharks had the highest taxonomic richness found among the 3 species, with 37 individual taxonomic groups found in their stomachs. The majority of the Atlantic sharpnose shark diet consisted primarily of teleost fishes, a group that was shared with blacktip sharks, with the most abundant fish taxon found being the family Sciaenidae. A study from the eastern and central GOM by Drymon et al. (2012) showed regional variance in Atlantic sharpnose shark diet using both stomach contents and stable isotope ratios, indicating a wide prey base. This trend in feeding corresponds to dietary information found in this study. While Atlantic sharpnose sharks showed very large taxonomic richness in their diet, they had a low species evenness and diversity. A consumer that exhibits trophic plasticity may have a large prey base but feeds opportunistically, taking advantage of less numerically available prey items to supplement their diet, whereas a feeder that has a less taxonomically diverse diet may feed evenly throughout its prey base, such as bonnetheads. Further evidence of the wide trophic niche of the Atlantic sharpnose shark was indicated by its low classification success using QDFA. Low classification success of Atlantic sharpnose sharks (24%) indicates a large amount of overlap with the other 2 species within the model, which was contrasted by high levels of classification in bonnetheads (93%), which had very little dietary overlap. Atlantic sharpnose sharks also had the lowest mean $\delta^{13}C$ values, indicating they fed the furthest offshore of the 3 species. They have been shown to have a relatively small home range, having a 95% estimated home range of <9 km (Carlson et al. 2008) as juveniles, little range separation via ontogeny (Bethea et al. 2015), and are thought to pup offshore (Drymon et al. 2010). These trends correlate to the low mean $\delta^{13}C$ values suggestive of offshore feeding where Atlantic sharpnose shark abundance is highest.

Establishing feeding patterns among migratory predators is crucial to understanding ecosystem dynamics and predator interactions. Assumptions that group species together as predators, ignoring differences in prey base and dietary trends, do not allow for accurate estimates of species influences on the ecosystem. This study suggests that all 3 species — Atlantic sharpnose, bonnethead, and blacktip shark — have different dietary preferences. This important distinction between species with significant range overlap can be used to provide estimates of their combined ecosystem influence throughout their range in the northwest GOM. Accurate estimates of feeding patterns can add crucial data to ecosystem models and provide useful information for ecosystem-based fishery management.

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