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Tyler Harrington

Texas A & M University - Galveston, tyler.harrington318@gmail.com

Jeff Plumlee

Texas A & M University - Galveston, jplumlee@tamu.edu

J. Marcus Drymon

University of South Alabama, Dauphin Island Sea Lab, mdrymon@disl.org

David Wells

Texas A & M University - Galveston, wells@tamug.edu

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DIETS OF ATLANTIC SHARPNOSE SHARK (*RHIZOPRIONODON TERRAENOVAE*) AND BONNETHEAD (*SPHYRNA TIBURO*) IN THE NORTHERN GULF OF MEXICO

Tyler Harrington^{1,2*}, Jeffrey D. Plumlee^{1,3}, J. Marcus Drymon^{4,5}, R. J. David Wells^{1,3}

¹Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, TX 77553; ³Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843; ⁴Department of Marine Sciences, University of South Alabama, Mobile, AL 36688; ⁵Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528; *Corresponding author, email: tharrington@fau.edu, ²Current address: Wildlife Epidemiology and Population Health Lab. Florida Atlantic University – Harbor Branch Oceanographic Institute, 5600 U.S. 1, Fort Pierce, FL 34946

ABSTRACT: Diets of two coastal sharks, Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) and Bonnethead (*Sphyrna tiburo*), were examined along the Texas and Alabama coasts in the northern Gulf of Mexico (GOM). Atlantic Sharpnose Sharks were collected from the northwest (n= 209) and northcentral (n= 245) GOM regions while Bonnetheads were collected from two locations within the northwest GOM (Galveston, Texas, n= 164; Matagorda, Texas, n= 79). Dietary analysis was conducted using stomach contents identified to the lowest taxonomic level, which were quantified using the index of relative importance (IRI) and non-parametric statistical analyses. Atlantic Sharpnose Sharks were revealed to be primarily piscivorous, with an overall %IRI of 79.76% for teleost fishes. Bonnetheads were shown to prey primarily on crustaceans (90.94% IRI), mainly crabs (22.06% IRI). Diets for Atlantic Sharpnose Sharks and Bonnetheads were evaluated by region and ontogeny, where variations by ontogeny were examined based on length at 50% maturity (L_{50}) values, delineating mature from immature individuals. Atlantic Sharpnose Sharks and Bonnetheads showed a decrease in dietary prey species richness from juveniles to adults using %IRI. Regional dietary differences existed with Atlantic Sharpnose Sharks from the northwest GOM consuming more crustaceans than conspecifics from the northcentral GOM. Bonnetheads collected from Galveston, TX consumed more crab than Bonnetheads from Matagorda, TX, while Bonnetheads from Matagorda, TX displayed a diet with higher prey species richness. Our results highlight differences in diets of two common shark species at both local and regional spatial scales.

KEYWORDS: stomach contents, feeding ecology, coastal sharks

INTRODUCTION

Predators play a critical role in the structure and function of marine ecosystems (Baum and Worm 2009). Removal of these predators, such as sharks, can cause negative effects on population structure and cascade to lower trophic levels throughout the food web (Heithaus 2008). Consequently, examining diets of predators can provide information about how an ecosystem functions and can potentially be affected by changing biotic and abiotic factors.

Quantification and description of diets of mesopredators can aid greatly in understanding geographical or seasonal changes in prey abundance and overall ecosystem connectivity (Cortés 1997). Spatial variability of prey abundance is common across marine ecosystems and can drive the distribution of predators (Kinney et al. 2011). However, common mesopredators that are ubiquitous throughout a system may exhibit temporal variability within their diet based on prey availability (Drymon et al. 2012). Geographic separation among populations of shark species that display regional variation in diet, such as the Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) (Drymon et al. 2012, Delorenzo et al. 2015) and Bonnethead (*Sphyrna tiburo*) (Betha et al. 2007), is important to consider when describing dietary preferences.

Atlantic Sharpnose Sharks and Bonnetheads are abun-

dant mesopredators in the northern Gulf of Mexico (GOM) (Drymon et al. 2010), share similar distributions (Drymon et al. 2013), and account for a large percentage of annual small coastal shark landings (Cortés 2005, 2009). Atlantic Sharpnose Sharks range from New Brunswick, Canada in the north to the Yucatan Peninsula in the south, including the GOM (Castillo–Geniz et al. 1998, Parsons and Hoffmayer 2005). Bonnetheads also have a widespread distribution, occurring in the coastal subtropical and tropical waters of the Pacific and Atlantic oceans surrounding the Americas (Castillo–Geniz et al. 1998). Both species are widely distributed throughout the GOM and undergo seasonal migrations that vary regionally and temporally (Parsons and Hoffmayer 2005). Atlantic Sharpnose Sharks and Bonnetheads exhibit similar life history traits, including small litter sizes and slow population growth rates (Castillo–Geniz et al., 1998; Fowler et al. 2005) making them vulnerable to overfishing. While frequently caught in recreational fisheries, these species also play an important role in commercial and artisanal fisheries. Atlantic Sharpnose Sharks account for 33% and 46% of annual small coastal shark commercial landings in the southeastern United States and annual small shark artisanal landings in Mexico, respectively (Cortés 2009). Bonnetheads

share a similar commercial importance and account for 50% of annual small coastal shark commercial landings in the southeastern United States and 15% of annual small shark artisanal landings in Mexico (Cortés 2005). A recent survey found Atlantic Sharpnose Sharks and Bonnetheads were the two most-captured shark species in the southern GOM off the coasts of Tabasco, Campeche, and Yucatan, Mexico (Pérez-Jiménez and Mendez-Loeza 2015).

Dietary information can be found for both Atlantic Sharpnose Sharks and Bonnetheads, but is limited in the northwest GOM. Atlantic Sharpnose Shark diets have been reported from the northcentral and northeastern GOM and contain a mixture of crustaceans, squid, and fish with fish as the primary dietary component (Bethea et al. 2004, Bethea et al. 2006, Drymon et al. 2012, Plumlee and Wells 2016). Bonnethead diets have also been evaluated in the northeastern GOM and northern Brazil with a specialized diet dominated by crustaceans, specifically *Callinectes* spp. crabs (Lessa and Almeida 1998, Bethea et al. 2007). Plant material has been observed in Bonnethead diets throughout all life stages (Cortés et al. 1996, Lessa and Almeida 1998, Bethea et al. 2007, Haman et al. 2012) where its presence may be due to incidental ingestion during pursuit of prey (Cortés et al. 1996).

Stomach content analysis is an effective tool to evaluate trophic interactions and provide snapshots of important prey items in the diets of predators (Cortés 1999). Given their ubiquity and commercial importance in the GOM, the goals of this study were to examine the feeding patterns of Atlantic Sharpnose Sharks and Bonnetheads along coastal regions of the northern GOM. The first objective was to use stomach content analysis to quantify the diets and identify the most important prey items to each species. Secondly, spatial and ontogenetic differences were examined. For Atlantic Sharpnose Sharks, diets were compared between the northwest and northcentral GOM (i.e. regional comparison) while Bonnethead diets were compared within the northwest GOM (Galveston, TX and Matagorda, TX, local comparison). Ultimately, quantifying and understanding the diets of two abundant shark species that reside in coastal waters of the northern GOM will provide a better understanding of species interactions and food web structure, which can be incorporated into ecosystem-based fisheries management plans.

MATERIALS AND METHODS

Sample Collections

Atlantic Sharpnose Sharks were collected from 2 regions in the GOM: northwest (off Galveston, TX) and northcentral (off Mobile, AL; Figure 1). Bonnetheads were opportunistically collected from 2 locations within the northwest GOM (Galveston and Matagorda, TX; Figure 1). All specimens from Galveston were obtained through recreational

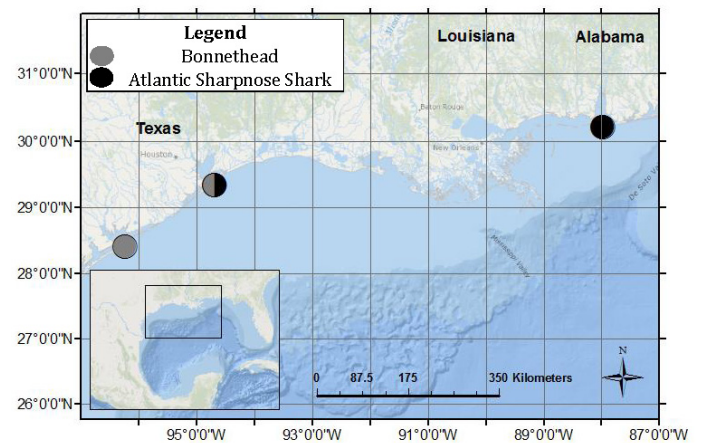


FIGURE 1. Map highlighting collection sites of Atlantic Sharpnose Shark and Bonnethead in the northern Gulf of Mexico. Dots indicate Mobile, AL, Galveston, TX, and Matagorda, TX from east to west.

headboat and private fishing vessels from April through October 2013. Shark stomach samples from Matagorda were collected from April to November 2013 through seasonal gill net sampling by the Texas Parks and Wildlife Department (TPWD). Stomach samples from the northwest GOM were removed onsite with data recorded for every specimen including total length (TL), fork length (FL), pre-caudal length (PCL), sex, and date of collection. Information such as trip time and bait type was obtained through personal correspondence with anglers and also recorded to ensure that sharks were captured within the region and that bait was not included in dietary calculations. Stomachs were transported to the laboratory where they were transferred into a 10% formalin solution for a minimum of 48 h, followed by a transfer to 70% ethanol for preservation until processing. Samples from the northcentral GOM were collected by longline surveys from 2006–2008 in the coastal waters of Alabama. A random stratified block design was used with 4 blocks, 2 west of 88° W and 2 east of 88° W, extending 37 km east to west from the shoreline to the 20 m isobaths as described in Drymon et al. (2012). Longlines were set for 1 h and sampling was replicated within each block along 3 depths: 0–5 m, 5–10 m, and 10–20 m. Six stations in one of the eastern and one of the western blocks were selected at random for monthly sampling. Measurements for samples from the northcentral GOM included weight, TL, FL, and PCL. Stomachs were removed and either frozen on the vessel or placed on ice and frozen upon return to the laboratory until processing.

Processing

Stomachs were processed in the laboratory using standard techniques. All stomachs were weighed (wet weight) to the nearest 0.1 g. Contents were then extracted with a series of 3 metal sieves with mesh sizes of 1.3 cm, 1400 μm , 500 μm , and a metal basin. Any material left in the metal basin was then run through a smaller sieve with mesh size of

50 μm and included as unidentified material. Contents in the remaining 3 sieves were placed in dissection trays to be sorted into respective groups. Stomach contents obtained from sharks caught by hook and line fishing from Galveston, TX were evaluated for hook holes and cross-referenced with information from angler interviews for identification of bait. Atlantic Mackerel was used as bait in sample collections from Mobile, AL. All contents identified as bait were not included in analysis. Prey items were identified to the lowest taxonomic level and cumulative prey curves (CPC) were developed for Atlantic Sharpnose Sharks and Bonnetheads from each region and location based on the number of prey items relative to the number of stomachs analyzed (Ferry and Cailliet 1996).

Data Analysis

Stomach contents were analyzed using standard metrics, including percent weight (%W), percent number (%N), percent frequency of occurrence (%O), and the index of relative importance (IRI) expressed as a percentage (%IRI). The IRI was determined as $\text{IRI} = \%O * (\%N + \%W)$ where %N is the number of items in a given stomach divided by the total number of items in that stomach, %W is the weight of a given item in a stomach divided by the total weight of the contents in that stomach, and %O is the number of stomachs that item occurred in divided by the total number of stomachs examined. To calculate IRI, the %N and %W were summed across all samples for each prey category. %IRI was then calculated as the IRI of a given prey item divided by the total IRI of all prey items. For further comparison, the %IRI data for each species was analyzed as a function of region and ontogeny. Atlantic Sharpnose Shark stomach contents were compared on a regional spatial scale between the northwest and northcentral GOM. Bonnethead data were compared on a local spatial scale within the northwest GOM (Galveston and Matagorda, TX). Changes in dietary habits with ontogeny were also investigated for each species based on length at 50% maturity (L_{50}) values to delineate immature from mature individuals (Carlson and Parsons 1997, Lombardi–Carlson et al. 2003, Fowler 2005, Hoffmayer et al. 2013, Frazier et al. 2014).

Further statistical analysis of stomach contents was accomplished using permutational analysis of variance (PERMANOVA) models. PERMANOVA models were based on a Bray–Curtis resemblance matrix and run using an unrestricted permutation of untransformed data. Stomach content analysis was accomplished by organizing the taxonomic groups found within the stomachs into higher categories. Highest level taxon was achieved at the subphylum and infraclass level (Teleostei, Crustacea, and Cephalopoda) while less common taxa were grouped into Other (Echinodermata, Bivalva, Gastropoda, indigestible material, and algae). When possible, prey items within the higher groups, Teleostei and Crustacea, were further classified using prey

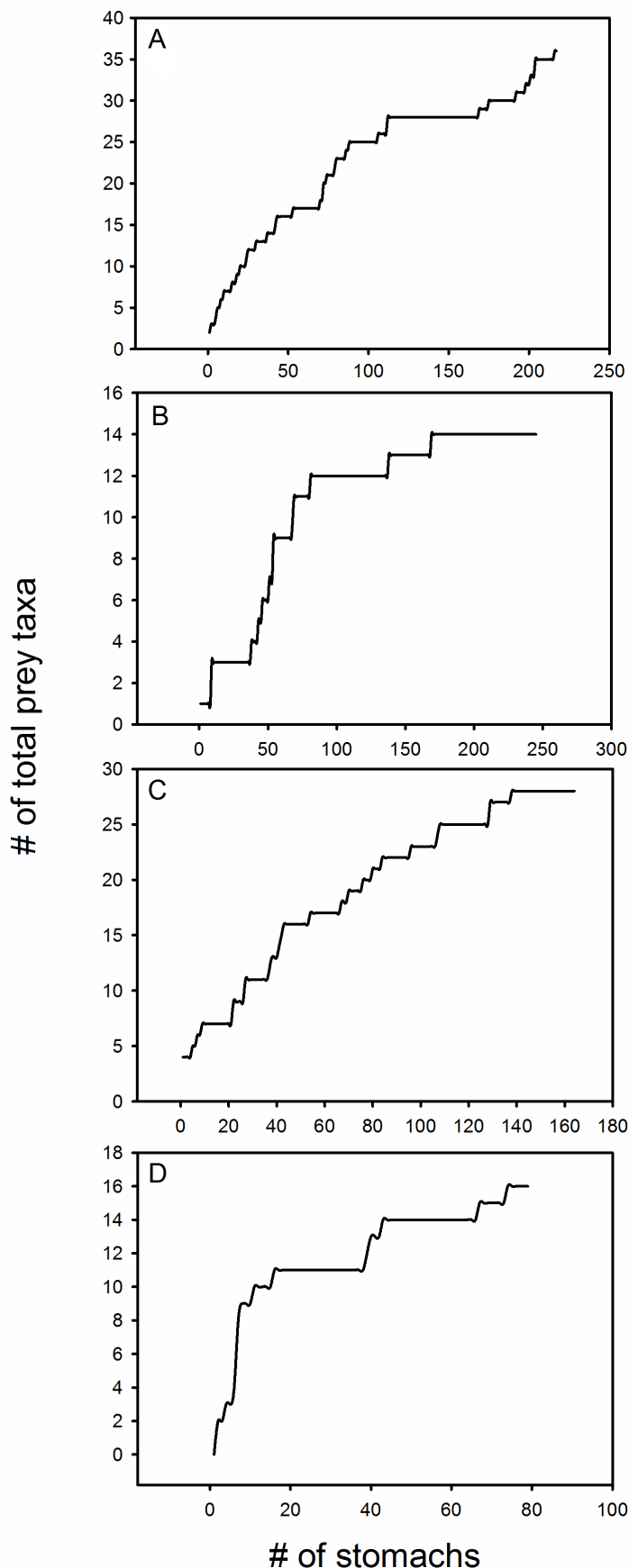


FIGURE 2. Cumulative prey curves generated for each shark species by region and location. A. Atlantic Sharpnose Shark (northwest Gulf of Mexico (GOM)). B. Atlantic Sharpnose Shark (northcentral GOM). C. Bonnethead (Galveston, TX). D. Bonnethead (Matagorda, TX).

groupings similar to those described in Bethea et al. (2004) and Bethea et al. (2007). Prey groupings included epibenthic teleost, pelagic teleost, penaeid shrimp, brachyuran, other crustaceans, cephalopods, and other (echinoderms, bivalves, gastropods, indigestible material, and algae). Unidentified material from groups Teleostei and Crustacea were removed from this analysis. Redefining the prey groupings excluded samples that had stomach contents only containing unidentified teleosts or crustaceans for both Atlantic Sharpnose Sharks (northwest GOM $n = 88$ and northcentral GOM $n = 41$) and Bonnetheads (Galveston Bay $n = 135$ and Matagorda Bay $n = 63$), yet increased taxonomic resolution of specifically important taxa to each species and region. Percent weight (%W) for each taxonomic group was used in these analyses given its significance in quantifying nutritional contribution (Rooker 1995). Similarity percentage (SIMPER) metrics were calculated to qualitatively determine differences of prey group contributions among factors. Significance was assessed at $\alpha \leq 0.05$, and all tests were run in PRIMER v.7 (Clarke and Gorley 2015).

RESULTS

A total of 697 stomach samples throughout the northern GOM were collected during this study. For Atlantic Sharpnose Sharks ($n = 454$), 209 were collected from the northwest GOM and 245 were collected from the northcentral GOM. For Bonnetheads ($n = 243$), 164 were collected from Galveston, TX while 79 were collected from Matagorda, TX. Cumulative prey curves indicated that each species and region had CPCs trending towards or meeting defined asymptotes (Figure 2).

Both Atlantic Sharpnose Sharks and Bonnetheads were collected across a wide range of sizes. Atlantic Sharpnose Sharks ranged in size from 36.7 – 90.5 cm FL with a mean

size of 71.8 ± 13.0 cm FL (Figure 3). A total of 119 juveniles and 335 adults were collected; 4 juveniles and 205 adults from the northwest GOM and 115 juveniles and 130 adults from the northcentral GOM. The mean weight of the stomach contents was 14.7 g, and 129 (18.5%) stomachs were empty. Bonnetheads had a mean length of 78.0 ± 11.9 cm FL and ranged in length from 49.0 – 102.0 cm FL (Figure 3). A total of 243 Bonnethead samples were collected; 126 adults and 38 juveniles from Galveston, TX and 23 adults and 54 juveniles from Matagorda, TX. Two individuals from Matagorda, TX lacked information on sex. Bonnetheads had a mean stomach content weight of 26.5 g, with one (0.4%) empty stomach. Among all stomach contents, 41 individual taxonomic groups were identified and 15 were identified to the species level. Atlantic Sharpnose Sharks had prey items representing 38 taxonomic groups, while Bonnetheads contained prey from 20 taxonomic groups.

Atlantic Sharpnose Shark diets consisted primarily of teleost fish (79.76% IRI) with contributions from crustaceans (8.09% IRI), cephalopods (2.58% IRI) and other material (10.61% IRI; Table 1, Figure 4). In lower taxonomic groupings, contributions came from teleost families such as Sciaenidae (0.19% IRI), Clupeidae (0.12% IRI), Engraulidae (0.08% IRI), Atherinidae (0.08% IRI), and Triglidae (0.04% IRI). Species identified included Gulf Menhaden (*Brevoortia patronus*, 0.14% IRI), Atlantic Cutlassfish (*Trichiurus lepturus*, 0.04% IRI), and Atlantic Croaker (*Micropogonias undulatus*, 0.01% IRI).

Atlantic Sharpnose Sharks from the northwest GOM had a diet primarily composed of teleost fish (77.61% IRI) and crustaceans (14.38% IRI). There were contributions from sciaenids (0.50% IRI), Gulf Menhaden (0.40% IRI), penaeid shrimp (3.05% IRI), and unidentified cephalopods (2.70% IRI). Diets of juvenile Atlantic Sharpnose Sharks

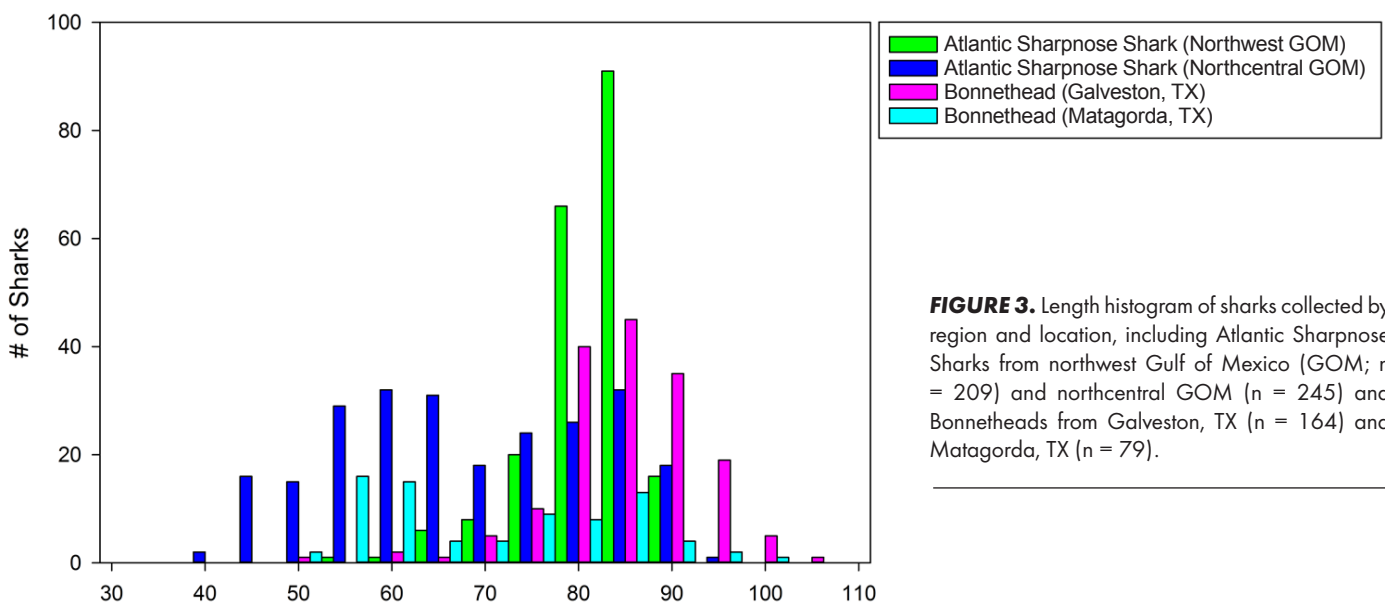


FIGURE 3. Length histogram of sharks collected by region and location, including Atlantic Sharpnose Sharks from northwest Gulf of Mexico (GOM; $n = 209$) and northcentral GOM ($n = 245$) and Bonnetheads from Galveston, TX ($n = 164$) and Matagorda, TX ($n = 79$).

TABLE 1. Atlantic Sharpnose Shark diet content by prey species category. Data expressed as percentage of Index of Relative Importance (%IRI).

Taxonomic Group	Identified Group	Lowest Taxonomic Group	Northcentral GOM			Northwest GOM			
			Overall %IRI	Total %IRI	Juvenile %IRI	Adult %IRI	Total %IRI	Juvenile %IRI	Adult %IRI
Teleost			79.76	78.26	74.33	79.34	77.61	26.41	78.35
	Unidentified Teleost		32.38	17.69	15.76	18.52	44.35	3.48	45.27
	Sciaenidae		0.19	0.01	-	0.01	0.50	-	0.51
		<i>Menticirrhus</i> spp.	<0.01	-	-	-	0.01	-	0.01
		<i>Menticirrhus littoralis</i>	<0.01	-	-	-	<0.01	7.07	-
		<i>Cynoscion arenarius</i>	<0.01	-	-	-	<0.01	-	<0.01
		<i>Micropogonias undulatus</i>	0.01	0.02	-	0.05	<0.01	-	<0.01
	Serranidae		<0.01	-	-	-	0.01	-	0.01
	Lutjanidae		<0.01	-	-	-	0.01	-	0.01
		<i>Lutjanus campechanus</i>	<0.01	0.01	0.05	-	<0.01	-	<0.01
	Scombridae		<0.01	-	-	-	<0.01	-	<0.01
	Carangidae		<0.01	-	-	-	0.01	-	0.01
		<i>Chloroscombrus chrysurus</i>	<0.01	-	-	-	<0.01	-	0.01
	Trichiuridae		-	-	-	-	-	-	-
		<i>Trichiurus lepturus</i>	0.04	-	-	-	0.12	-	0.12
	Gobiidae		-	-	-	-	-	-	-
		<i>Gobioides broussonetii</i>	<0.01	-	-	-	<0.01	-	<0.01
	Sparidae		-	-	-	-	-	-	-
		<i>Archosargus probatocephalus</i>	<0.01	-	-	-	<0.01	-	<0.01
	Paralichthyidae		<0.01	-	-	-	<0.01	-	<0.01
	Clupeidae		0.12	0.01	-	0.02	0.28	-	0.29
		<i>Brevoortia patronus</i>	0.14	-	-	-	0.40	-	0.41
	Engraulidae		0.08	0.12	0.70	<0.01	0.05	-	0.05
	Mugilidae		<0.01	-	-	-	<0.01	-	<0.01
	Ariidae		<0.01	<0.01	0.02	-	<0.01	-	<0.01
	Atherinidae		0.08	0.50	0.07	0.89	-	-	-
	Triglidae		0.04	0.18	0.03	0.31	-	-	-
		<i>Symphurus plagiusa</i>	<0.01	0.01	0.07	-	-	-	-
Crustacea			8.09	1.95	4.64	0.94	14.38	66.63	13.66
	Unidentified Crustacea		0.59	-	-	-	1.73	3.21	1.70
	Penaeidae		1.72	0.38	1.47	0.08	3.05	41.60	2.72
	Sicyoniidae		-	-	-	-	-	-	-
		<i>Sicyonia brevirostris</i>	0.01	0.04	0.07	0.02	-	-	-
	Unidentified Brachyura		0.18	0.16	0.54	0.05	0.19	-	0.20
	Portunidae		0.01	-	-	-	0.01	-	0.02
		<i>Callinectes similis</i>	0.01	-	-	-	0.03	-	0.03
	Xanthidae		<0.01	-	-	-	-	-	-
	Stomatopoda		0.15	0.28	0.93	0.09	0.10	5.13	0.07
		<i>Squilla empusa</i>	<0.01	-	-	-	<0.01	-	<0.01
Cephalopoda			1.54	0.47	2.91	0.01	2.58	5.28	2.51
	Unidentified Cephalopoda		0.02	0.19	0.96	0.01	-	-	-
	Unidentified Teuthoidea		0.91	-	-	-	2.70	5.28	2.51
		Loliginidae	<0.01	0.01	0.07	-	-	-	-
Other			10.61	19.32	18.12	19.71	5.44	1.68	5.48
	Gastropoda		<0.00	0.01	-	0.03	-	-	-
	Algae		<0.01	-	-	-	<0.01	-	<0.01

from the northwest GOM were mixed between teleost (26.41% IRI), crustaceans (66.63% IRI), and cephalopods (5.28% IRI) and adults shared the same primary components with a diet shift to a higher contribution from teleosts (78.35% IRI), and lower contributions from crustaceans (13.66% IRI) and cephalopods (2.51% IRI).

In the northcentral GOM, Atlantic Sharpnose Sharks

showed a more teleost-dominated diet (78.26% IRI) with a lower contribution from crustaceans (1.95% IRI) and a larger amount of the other category (19.32% IRI). Juveniles from the northcentral GOM had contributions from teleosts (74.33% IRI), crustaceans (4.64% IRI), and other (18.12% IRI), while adults shifted primarily to teleosts (79.34% IRI) and other (19.71% IRI; Table 1). Other regional differences

included the presence of fish from families Clupeidae and Trichiuridae in the northwest GOM in contrast to fish from families Atherinidae and Triglidae present only from samples in the northcentral GOM.

Bonnethead diets were composed almost entirely of crustaceans (90.94% IRI) with a small contribution from other (8.11% IRI), primarily consisting of algae (7.44% IRI; Table 2, Figure 4). Among prey identified to lower taxonomic levels, contributions included unidentified brachyurans (22.06% IRI), blue crab (*Callinectes sapidus*) (2.19% IRI), and stomatopods (2.35% IRI). Bonnetheads from Galveston, TX showed a large dietary contribution of crustaceans (94.61 %IRI) with only algae (4.22% IRI) within the other category contributing more than 1% IRI. Between juvenile and adult Bonnetheads in Galveston, TX crustaceans remained the major contributor (96.59% IRI and 92.41% IRI, respectively) and there was a decrease in the contribution from teleosts (1.87% IRI juvenile and 0.45% IRI adult) and an increase in the contribution from other material (1.21% IRI juvenile and 6.45% IRI adults) with increasing size and age. In Matagorda, TX, crustaceans contributed most to the diet (79.67% IRI), but there was a large increase in the observed contribution of other (19.78% IRI) compared to Galveston, TX. Ontogenetically, Bonnetheads from Matagorda, TX showed an increase in the contribution of crustaceans from juveniles to adults (77.83% IRI and 81.81% IRI, respectively), while the contribution from other material decreased (21.46% IRI juveniles and 16.74% IRI adults; Table 2).

Significant differences between Atlantic Sharpnose Sharks and Bonnetheads existed using the overall prey species taxonomic groupings from all sharks combined (PERMANOVA; Pseudo-F = 320.27, permutated p-value ≤ 0.05), and prey species sub-groupings from samples that did not solely contain unidentified teleosts and crustaceans (Pseudo-F = 102.32, permutated p-value ≤ 0.05). Teleost was most important for Atlantic Sharpnose Sharks versus Bonnetheads (SIMPER; mean \pm sd dissimilarity = 33.86 ± 1.59) and crustacean was most important for Bonnetheads versus Atlantic Sharpnose Sharks (SIMPER; dissimilarity = 33.70 ± 1.66 sd). Further analysis using sub-groupings (epibenthic teleost, pelagic teleost, penaeid shrimp, brachyuran, other crustaceans, cephalopods, and

other) indicated that the group most differentiating Atlantic Sharpnose Sharks from Bonnetheads was pelagic teleosts (SIMPER; dissimilarity = 13.22 ± 0.63), whereas the prey category most separating Bonnetheads from Atlantic Sharpnose Sharks was crabs (SIMPER: dissimilarity = 34.23 ± 1.79).

Regional differences in Atlantic Sharpnose Shark diet were found between individuals collected in the northwest vs. the northcentral GOM using overall groupings (PERMANOVA; Pseudo-F = 3.82, permutated p-value ≤ 0.05); however, not for prey species sub-groupings (PERMANOVA; Pseudo-F = 1.83, permutated p-value > 0.05). Specifically, higher %W of teleost prey was found in the northcentral GOM compared to the northwest GOM (SIMPER; dissimilarity = 20.81 ± 0.95) and higher %W of crustaceans in the northwest GOM (SIMPER; mean abundance 29.80%) relative to the northcentral GOM (SIMPER; mean abundance 18.10%). For Bonnetheads, no significant location effect was found between sharks collected from Galveston, TX and Matagorda, TX using overall prey species groupings (PERMANOVA, Pseudo-F = 2.98, permutated p-value > 0.05); however, a significant location effect was found for sub-groupings excluding unidentified Teleost and unidentified Crustaceans (PERMANOVA, Pseudo-F =

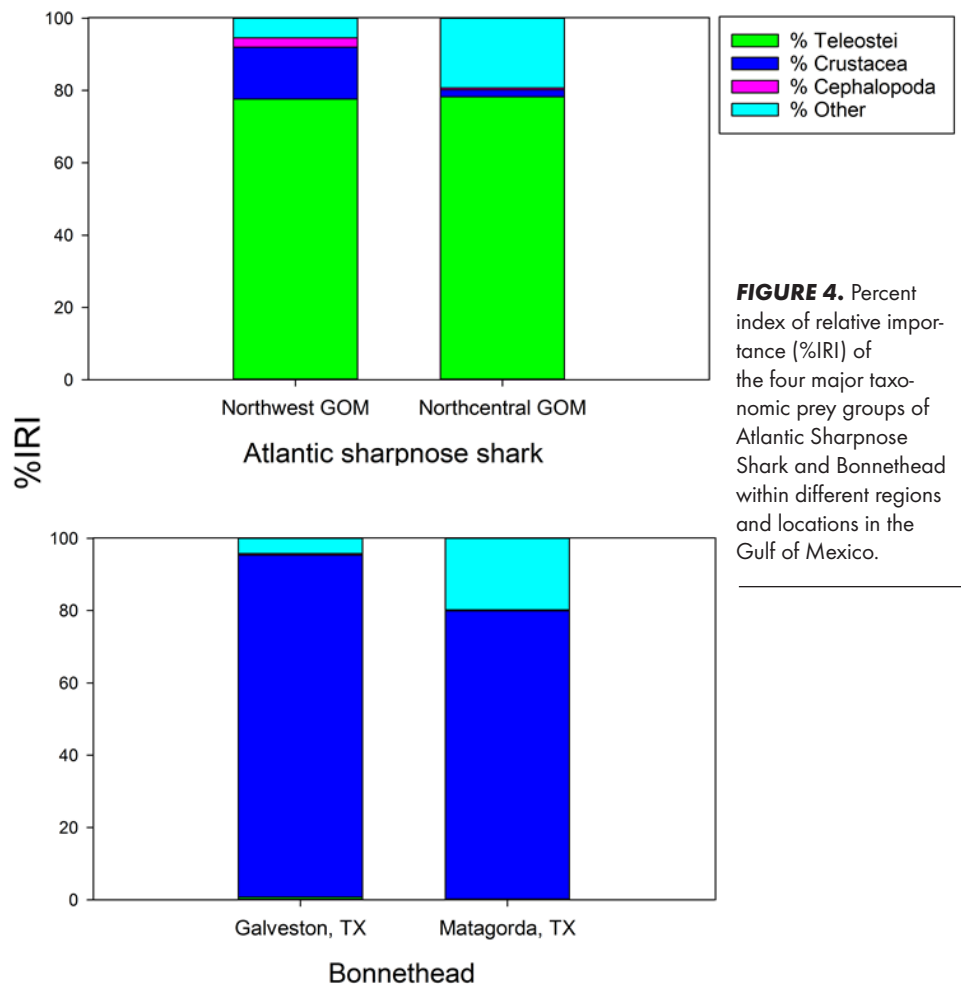


FIGURE 4. Percent index of relative importance (%IRI) of the four major taxonomic prey groups of Atlantic Sharpnose Shark and Bonnethead within different regions and locations in the Gulf of Mexico.

TABLE 2. Bonnethead diet content by prey species category. Data expressed as percentage of Index of Relative Importance (%IRI).

Taxonomic Group	Identified Group	Lowest Taxonomic Group	Matagorda, TX				Galveston, TX		
			Overall %IRI	Total %IRI	Juvenile %IRI	Adult %IRI	Total %IRI	Juvenile %IRI	Adult %IRI
Teleost			0.56	0.23	0.02	0.99	0.74	1.87	0.45
	Unidentified Teleost		0.35	0.24	0.02	0.84	0.41	0.50	0.35
	Sciaenidae		<0.01	-	-	-	<0.01	0.03	-
	Clupeidae		<0.01	-	-	-	<0.01	0.04	-
		<i>Brevoortia patronus</i>		<0.01	-	-	<0.01	-	0.01
	Mugilidae		<0.01	-	-	<0.01	0.05	-	
Crustacea			90.94	79.67	77.83	81.81	94.61	96.59	92.41
	Unidentified Crustacea		6.19	4.76	4.86	-	6.73	4.78	8.40
	Penaeidae		0.10	0.03	0.11	-	0.14	0.01	0.20
		<i>Penaeus setiferus</i>		0.01	0.01	0.06	-	<0.01	0.04
	Unidentified Brachyura		22.06	16.87	11.95	29.69	24.24	18.43	25.90
	Portunidae		1.23	1.64	2.20	0.28	1.00	4.69	0.37
		<i>Callinectes sapidus</i>		2.19	2.02	6.49	-	2.22	3.62
		<i>Callinectes similis</i>		0.10	0.04	0.09	-	0.12	0.05
		Xanthidae		0.02	0.02	0.10	-	0.02	0.09
		Stomatopoda		2.35	2.41	2.56	1.96	2.27	2.58
		<i>Squilla empusa</i>		0.06	0.06	0.24	-	0.07	0.17
Cephalopoda			0.39	0.31	0.69	0.46	0.42	0.32	0.69
	Unidentified Cephalopoda		0.03	0.31	0.69	0.46	-	-	-
	Unidentified Teuthoidea		0.20	-	-	-	0.42	0.51	0.58
Other			8.11	19.78	21.46	16.74	4.23	1.21	6.45
	Bivalvia		<0.01	0.01	0.04	-	-	-	-
	Gastropoda		0.01	<0.01	-	-	-	-	-
	Algae		7.44	18.14	4.31	15.10	4.22	4.04	4.36

5.65, permuted p -value ≤ 0.05). The most important prey groups contributing to the differences in Bonnetheads were higher %W of crab in Galveston, TX versus Matagorda, TX (SIMPER; dissimilarity = 19.70 ± 1.04) and higher %W of other in Matagorda, TX relative to Galveston, TX (SIMPER; dissimilarity = 12.65 ± 0.68).

DISCUSSION

Differences in the diets of 2 co-occurring mesopredators were demonstrated, suggesting some degree of resource partitioning. Atlantic Sharpnose Sharks and Bonnetheads in this study displayed distinct dietary contributors, fish and crab, respectively. Atlantic Sharpnose Shark diets contained a wider range of prey items while Bonnetheads displayed a specialized diet of crustaceans, primarily consisting of crabs.

Atlantic Sharpnose Shark diets in the northwest and northcentral GOM displayed a propensity for teleost fish, but higher contributions from both crustaceans and cephalopods occurred in the northwest GOM. Previous studies have shown similar dietary variations suggesting a generalist diet for Atlantic Sharpnose Sharks with fish as the primary contributor (Gelsleichter et al. 1999, Bethea et al. 2006, Drymon et al. 2012). Further analysis of Atlantic Sharpnose Shark diets showed a reduction in dietary species richness from juveniles to adults. A large loss in the dietary contribution of

crustaceans and squid in both regions suggests a refinement in diet with maturity, which is supported from previous findings (Bethea et al. 2007, Plumlee and Wells 2016). Minor differences between regions were observed at the teleost family level between the northwest and northcentral GOM. Regional variance in the dietary composition of teleost prey in Atlantic Sharpnose Sharks is frequently documented (Barry 2002, Bethea et al. 2006, Drymon et al. 2012) and likely related to the fish assemblage of a given ecosystem. Due to the high diversity of contents found in Atlantic Sharpnose Shark stomachs, our findings suggest Atlantic Sharpnose Sharks in the northwest and northcentral GOM are generalist predators, consuming a wide range of prey items that are likely dependent on the prey species composition of the region in which they are found.

Bonnetheads showed a consistent diet composed almost entirely of crustaceans with similar contributions, both geographically and ontogenetically, from Portunid crabs, xanthid crabs, and stomatopods. The results from this spatial comparison support and elucidate results from previous studies in other regions (Cortés et al. 1996, Lessa and Almeida 1998, Bethea et al. 2007) showing that blue crabs (*Callinectes* spp.) were the dominant dietary prey species for Bonnetheads. Samples collected from Galveston had a higher presence of penaeid shrimp and a lower presence in the cat-

egory other compared to samples from Matagorda, though these differences can be considered negligible. Bay systems, such as those found in Matagorda and Galveston, TX, serve as nursery grounds to many crustacean species (Beck et al. 2001, Minello et al. 2008). The slight differences observed in Bonnethead stomach contents between these 2 locations are most likely influenced by the variety of crustacean species that utilize these areas as nursery grounds. Nevertheless, the crustacean assemblages near each bay system evaluated in this study had little effect on the overall diet composition. Bonnetheads within the northwest GOM have been confirmed to be specialized predators showing little to no dietary variation beyond *Callinectes* spp. crabs.

The observed dietary differences are also driven by morphology. Many crustacean prey items found in Bonnethead stomachs in this study were comparatively large, whole, and easily identified to lower taxonomic levels. Bonnetheads have a highly modified head structure characteristic of the family Sphyrnidae (hammerhead family). The enlarged cephalofoil offers an enhanced electro-sensory system compared to sharks in the family Carcharhinidae (requiem sharks), which is used to detect concealed prey items (McComb et al. 2009). Bonnetheads also display an enlarged maximum gape but a lower maximum bite force (Wilga and Motta 2000, Mara et al. 2010, Rice et al. 2016). This, along with posterior molariform teeth, asynchronous muscle activity, tooth reorientation during biting, and prolonged jaw

adductor activity patterns, allows for prey crushing and suction during feeding, making the Bonnethead an extremely efficient durophagous predator (Mara et al. 2010). Carcharhinid sharks, such as Atlantic Sharpnose, lack many of these traits, allowing Bonnetheads to exploit preferred prey items (crabs) more effectively and reduce the amount of competition from similar sized sharks.

Atlantic Sharpnose Sharks have been found to be pelagic, generalist predators with consistent, fish-dominated diets and varied contributions of taxa based upon region of collection (Drymon et al. 2012). In contrast, Bonnetheads demonstrate more benthic, specialized feeding strategies with consistent diets among various regions (Cortés et al. 1996, Lessa and Almeida 1998, Bethea et al. 2007, Bethea et al. 2011, Haman et al. 2012). This study evaluated the diets of these two species at spatial scales not previously compared and found similar results to studies conducted in singular locations. Analysis beyond traditional stomach contents (e.g., DNA barcoding) would likely increase resolution and provide insight on the prevalence of prey species in the diets of sharks, which may be dependent on ecosystem assemblages in a given region. Regional comparisons of the diets of common sharks allow for more extensive evaluations of species-wide dietary preferences. Such evaluations are important to further the understanding of the role of predators in marine ecosystems, information crucial to effective ecosystem-based fisheries management.

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