Diet of the bonnethead (*Sphyrna tiburo*) along the northern Gulf of Mexico and southeastern Atlantic coast of the United States

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Abstract

*Diet of the bonnethead (*Sphyrna tiburo*) along the northern Gulf of Mexico and southeastern Atlantic coast of the United States*. The diet of a potentially omnivorous coastal shark species, the bonnethead (*Sphyrna tiburo*), was examined in the western Atlantic along the coast of the southeastern United States. A total of 423 stomachs collected from Texas, Alabama, Florida and South Carolina were analyzed using standardized stomach content analysis methods. The diet was dominated by crabs, primarily portunids (*Callinectes* spp.), across the geographical range analyzed, though the relative importance of crabs varied between regions. Ontogenetic shifts in diet were not observed throughout the region studied. Female and male bonnetheads in South Carolina displayed different diets, particularly in the amount of portunid crabs consumed, with a higher proportion ingested by females. Bonnetheads consumed limited amounts of seagrasses in all regions except in South Carolina, where they occupy habitats without seagrasses in marsh dominated bays and estuaries. This finding indicates that, at least seasonally, seagrasses are not an essential part of the diet of this shark species and may only occur in stomachs as accidental ingestion.

Key words: Elasmobranch diet, Feeding ecology, *Sphyrna tiburo, Callinectes* spp., Seagrasses

Resumen

*La dieta de la cornuda de corona (*Sphyrna tiburo*) en el norte del golfo de México y la costa atlántica del sureste de los Estados Unidos de América.* Se estudió la dieta de un tiburón costero potencialmente omnívoro, la cornuda de corona (*Sphyrna tiburo*), en el Atlántico occidental a lo largo de la costa suroriental de los Estados Unidos de América. Se procesaron los estómagos de 423 ejemplares capturados en Tejas, Alabama, Florida y Carolina del Sur utilizando métodos estandarizados de análisis de contenido estomacal. En la zona geográfica estudiada, predominaron los cangrejos, principalmente portúnidos (*Callinectes* spp.), aunque la proporción relativa de los cangrejos varió entre regiones. No se observaron cambios ontogenéticos en la dieta en la región estudiada. Se observaron diferencias en las dietas de las hembras y los machos de cornuda de corona en Carolina del Sur, sobre todo por la cantidad de cangrejos portúnidos consumidos, que fue mayor en las hembras. Las cornudas de corona consumieron cantidades limitadas de praderas submarinas en todas las regiones excepto en Carolina del Sur, donde los tiburones ocupan bahías y estuarios en marismas donde no existen tales praderas. Todo ello indica que, al menos temporalmente, las praderas submarinas no son una parte importante de la dieta de esta especie de tiburón y que su presencia en los estómagos podría ser tan solo el resultado de la ingestión accidental.

Palabras clave: Dieta elasmobranquios, Ecología alimentaria, *Sphyrna tiburo*, *Callinectes* spp., Praderas submarinas

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Introduction

The bonnethead (*Sphyrna tiburo* L.) is a small coastal shark that inhabits the continental margins of the tropical and subtropical Atlantic waters of North and South America, from the Chesapeake Bay, United States to Brazil, including the Gulf of Mexico (GOM) (Ebert et al., 2021). Along coastlines of the GOM and the southeastern United States, bonnetheads are among the most abundant of coastal shark species and can tolerate high variation in salinities (16–38 ppt) (Ulrich et al., 2007; Bethea et al., 2008). The migratory habits of bonnetheads vary across their range and are poorly understood throughout most of the GOM. Bonnetheads in southwest Florida are thought to have limited migrations, and latitudinal variation in growth has been observed along the western Florida coastline (Parsons, 1993). On the U.S. Atlantic coast in the higher latitude waters of South Carolina, bonnetheads exhibit temperature driven migrations, spending summer months in South Carolina and winter months in warmer waters off the eastern coastline of Florida (Driggers et al., 2014). Sexual segregation has been observed in South Carolina with higher abundance of female bonnetheads in estuaries (Ulrich et al., 2007; Driggers et al., 2014). These individuals display intra–and interannual high site fidelity, with almost all tagged fish in South Carolina estuaries recaptured within and between years at the same estuary of initial capture (Driggers et al., 2014). Similar site fidelity has been found in Charlotte Harbor, Florida, and although migration likely occurs, migratory data are lacking (Heupel et al., 2006).

Population structure of bonnetheads along the southeastern and GOM coast of the U.S. is not fully understood. A recent study by Díaz–Jaimes et al. (2021) found significant population structure between the Atlantic and eastern GOM, as well as between these regions and the southern GOM; however, the study lacked samples from the northern and western GOM. Several other species of small coastal sharks have been found to have distinct population structure both between the Atlantic and GOM coasts of the United States as well as within the GOM (Keeney et al., 2003; Portnoy et al., 2014, 2016). Ongoing genetic work indicates an Atlantic population and two populations of bonnetheads within the U.S. GOM (eastern and western) with a geographic midpoint around 87.5°W (Portnoy et al., unpublished data).

Bonnetheads are considered dietary specialists feeding mostly on crabs when in estuaries (Kroetz et al., 2017). Crabs in the genus *Callinectes* are especially important in bonnethead diet, comprising most crabs identified in stomach contents (Cortés et al., 1996; Lessa and Almeida, 1998; Plumlee and Wells, 2016). Blue crabs (*Callinectes sapidus*) are distributed in coastal and estuarine waters in the western Atlantic from Nova Scotia (Canada) to northern Argentina (Williams, 1974). The abundance of juvenile *Callinectes sapidus* in GOM, Florida and southeastern Atlantic coastline seem to follow density–independent patterns and are synchronized with environmental factors (Sanchez–Rubio et al., 2011; Colton et al., 2014). Foraging opportunities may be one of the factors driving seasonal migration of bonnetheads along the east coast of North America. Driggers et al. (2014) suggested that high site fidelity observed in bonnetheads in South Carolina is driven by a seasonally abundant stock of blue crabs (*Callinectes sapidus*), with ovigerous female blue crabs providing the nutrients necessary for rapid (4.5 month, Gonzalez de Acevedo et al., 2020) embryo development in mature female bonnetheads.

Several studies have found and enumerated seagrasses (aquatic angiosperm plants) in the stomachs of bonnetheads but attributed them to accidental ingestion (Cortés et al., 1996; Kroetz et al., 2017). The presence of seagrass in bonnethead stomachs does not necessarily indicate omnivory; however, Leigh et al. (2018) found that bonnetheads fed seagrasses in captivity were able to assimilate seagrass nutrients into their tissue, suggesting omnivory is possible in the species. This finding, coupled with the high abundance of seagrasses in the diet of bonnetheads observed in some regions (Bethea et al., 2007), indicates that seagrasses may play a nutritional role in the species, at least during the immature life stage when seagrasses are more frequently found in stomach contents (Bethea et al., 2007; Kroetz et al., 2017). However, bonnetheads feed commonly on benthic prey found in proximity to seagrass beds, and other species of sharks with similar feeding strategies have been found to incidentally consume seagrass as well (Cortés and Gruber, 1990; Cortés et al., 1996; Bethea et al., 2007). Additionally, seagrasses are not ubiquitous throughout the range of bonnetheads, as no seagrasses occur in the turbid *Spartina* spp. marsh ecosystem on the Atlantic coastline of South Carolina (Dame et al., 2000; Green and Short, 2003).

The diet of bonnethead sharks has been well characterized in the GOM. In western Florida, bonnethead diet varies by season and habitat, but is nonetheless generally dominated by crabs, with seagrasses being the second most common observed stomach content (Cortés et al., 1996; Bethea et al., 2007). Bonnethead diet is also geographically variable in western Florida, with crabs generally being the most prevalent prey, although other crustaceans and cephalopods dominate bonnethead diet in southwestern Florida (Bethea et al., 2007). Juveniles in western Florida and the adjacent waters of Alabama show higher ingestion rates of seagrasses as compared to adults in the same locations (Bethea et al., 2007; Kroetz et al., 2017). Bonnetheads in Alabama have similar feeding habits to western Florida, but their diet also includes shrimp (Kroetz et al., 2017). The diet of bonnetheads in northern Brazil and the western GOM waters (Texas) is also dominated by crabs, with no seagrasses noted in stomach contents (Lessa and Almeida, 1998; Plumlee and Wells, 2016). Prior to the current study, diet of bonnetheads along the U.S. east coast had not been examined.

This study aims to complement previous dietary studies of bonnetheads and provide novel data on their diet from the seasonally migratory North Atlantic populations found in South Carolina and eastern Florida

Table 1. Number of mature and immature bonnethead (*Sphyrna tiburo*) stomachs analyzed, as well as mean length and size ranges (mm fork length, FL) for each location sampled.

*Tabla 1. Numero de estómagos analizados de ejemplares adultos y juveniles de cornuda de corona (*Sphyrna tiburo*), longitud media y rango de talla (longitud de la horquilla en mm, FL) en cada localidad estudiada.*

Location	Maturity	N	Mean FL	Max FL	Min FL
Texas	Immature	132	522	805	334
	Mature	10	780	889	632
Alabama	Immature	1	753	753	753
	Mature	36	872	1,015	670
Northwest Florida	Immature	45	520	750	390
	Mature	50	665	900	560
West–central Florida	Immature	18	490	600	360
	Mature	12	753	810	595
East Florida	Immature	10	494	845	265
	Mature	8	796	994	620
South Carolina	Immature	41	583	865	364
	Mature	56	835	1,035	656

estuaries. By comparing the diet of sharks collected in the estuaries of South Carolina and eastern Florida with sharks collected from multiple locations within the GOM, we further characterize regional differences in the feeding ecology of bonnetheads.

Material and methods

Bonnetheads were collected during fishery–independent surveys from two Atlantic sites on the U.S. east coast: South Carolina (32.4°N –80.4°W to 33.0°N –79.5°W) and eastern Florida (27.9°N –80.6°W to 28.0°N –80.8°W), and four sites in the GOM: Texas (26.2°N –97.4°W to 29.3°N –95.2°W), Alabama (29.1°N –88.5°W to 30.3°N –87.5°W), northwest Florida (28.3°N –82.8°W to 30.1°N –84.1°W) and west central Florida (27.3°N –82.6°W to 27.4°N –82.6°W) (table 1). Seagrasses occur in all regions sampled except for South Carolina (Green and Short, 2003). Bonnetheads were collected primarily by gillnet from 2012 to 2019, however samples were also collected with other gears (longlines, seine, and trawl nets). Sharks were sexed and measured to the nearest centimeter (cm) for fork and total length upon capture, and maturity status was macroscopically determined when possible (table 1). If maturity was not determined at capture, maturity was assigned based on region–specific length at maturity estimates. Female and male bonnetheads from South Carolina were considered mature at 819 mm and 618 mm fork length, respectively (Frazier et al., 2014). Female and male bonnetheads from the GOM were considered mature at 944 mm and 830 mm total length, respectively (Lombardi–Carlson et al., 2003). Stomachs were excised from sharks, bagged, and frozen until analysis.

In the laboratory, stomachs were thawed, opened with scissors and contents were collected in a sieve (335 µm mesh). The sieve was lightly rinsed to remove excess mucus, contents were transferred to a sorting dish and identified to the lowest taxon possible under a dissecting scope. Each prey item was counted and weighed to the nearest 0.001 g (wet weight). From sharks collected using longlines, any stomach contents identified as bait were removed. Prey items were then grouped into one of eight categories for analysis: crabs, shrimp, stomatopods, cephalopods, teleost fishes, seagrasses, macroalgae, and other arthropods.

Standard stomach content indices were calculated as the index of relative importance (Hyslop. 1980):

$$IRI = (\%N + \%W) \times FO$$

where FO is the frequency of occurrence, %N the percent number, %W the percent weight of contents.

A percent index of relative importance (%IRI) was calculated according to the formula (Cortés, 1997):

$$\%IRI = (IRI_{Category} / IRI_{Total}) \times 100$$

where $IRI_{Category}$ is the IRI for a prey category and IRI_{Total} refers to the sum of IRIs from each category. Percent IRI of each prey category was calculated for mature and immature sharks of each site. In South Carolina, mature and immature sample %IRI was

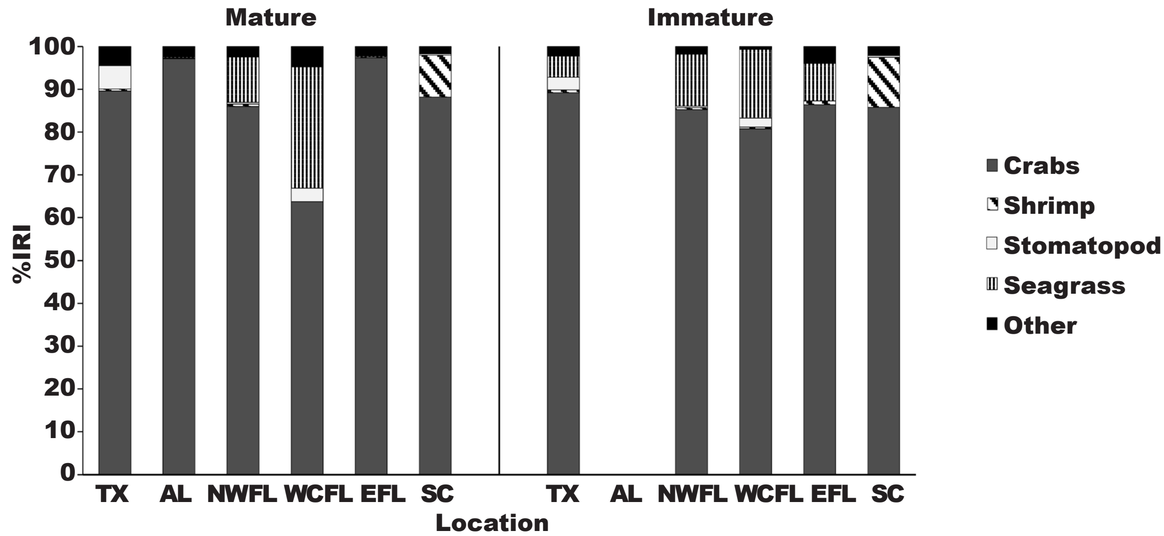

Fig. 1. %IRI contributions of each major prey group to both mature and immature bonnetheads (*Sphyrna tiburo*) from Texas (TX), Alabama (AL), northwest Florida (NWFL), west central Florida (WCFL), eastern Florida (EFL), and South Carolina (SC). Prey groups contributing to < 5 % of diet (cephalopods, macroalgae, and other arthropods) have been combined into 'Other' category.

*Fig. 1. Contribuciones al porcentaje del indicador de importancia relativa (%IRI) de cada grupo de presas a los ejemplares maduros e inmaduros de las cornudas de corona (*Sphyrna tiburo*) de Tejas (TX), Alabama (AL), Florida nororiental (NWFL), Florida centrooccidental (WCFLI), Florida oriental (EFL), y Carolina del Sur (SC). Los grupos de presas que representan < 5 % de la dieta (cefalópodos, macroalgas y otros artrópodos) se han agrupado en la categoría "Other".*

calculated for each unique taxon of prey to provide a detailed description of their diet. In addition, % IRI of each prey taxon was calculated for male and female bonnetheads, regardless of maturity, in South Carolina to examine potential differences in diet due to sexual segregation.

All statistical analyses were conducted in R Studio version 1.3.1093 (R Studio Team, 2020). For statistical analysis, samples were combined into three populations indicated by genetic analyses in the U.S. GOM and Atlantic (Portnoy et al., unpubl. data). These three groups are the western GOM (–97.5º to –88.0º longitude; Texas to Alabama; n = 179), the eastern GOM (–88.0º to –80.5º longitude; northwest and west central Florida ; n = 125), and the Atlantic, encompassing coastal waters from South Carolina to eastern Florida (n = 114). Species accumulation curves were generated for each regional group. These curves were used to assess whether the number of samples in each group was sufficient to accurately depict the diet of the region. Data were square root transformed and compiled into a Bray–Curtis dissimilarity matrix. A permutational multivariate analysis of variance (PERMANOVA) was used to test whether diets (%W) varied significantly ($p < 0.05$) between each combination of regions (western GOM with eastern GOM, western GOM with Atlantic, eastern GOM with Atlantic). Each PERMANOVA result was tested by the betadisper function followed by an analysis of variance (ANOVA) to assess whether significant differences observed in the PERMANOVA were due to location (alpha diversity) or dispersion effects (beta diversity). A non–significant ($p > 0.05$) ANOVA result indicated that differences between groups were due to location effects. Finally, a similarity percentage (SIMPER) test was used to identify the contribution of individual prey groups to the differences observed in regional diets.

Results

In total, 423 bonnethead stomachs were analyzed. Of these 144 (two empty) were from Texas, 37 were from Alabama, 96 (one empty) were from northwest Florida, 18 were from east Florida, 30 were from west central Florida, and 97 (one empty) were from South Carolina (table 1). Empty stomachs (n = 4,1 % of total stomachs analyzed) were excluded from further diet analyses.

The diet of immature bonnetheads was similar across all areas sampled (fig. 1). Crabs, primarily the family Portunidae, dominated bonnethead diet in each region sampled but were most prevalent in the diet of immature individuals from Texas (89.2 %IRI). Shrimp were an abundant prey item only in juvenile bonnetheads from South Carolina (11.7 %IRI; fig. 1). Seagrasses, primarily *Thalassia testudinum* and *Halodule wrightii*, were found in stomachs of immature bon-

Table 2. Stomach contents from South Carolina bonnetheads (*Sphyrna tiburo*) reported to the lowest identified taxa as %IRI. Mature (n = 56), immature (n = 40), male (n = 36) and female (n = 60) individuals are shown.

*Tabla 2. Contenido estomacal de los ejemplares de cornuda de corona (*Sphyrna tiburo*) en Carolina del Sur identificado hasta el menor nivel taxonómico como %IRI (porcentaje del índice de importancia relativa). Se presentan datos de individuos adultos (n = 56), inmaduros (n = 40), machos (n = 36) y hembras (n = 60).*

Prey		Mature	Immature	Male	Female
Crabs	*Callinectes sapidus*	76.56	71.65	26.81	87.66
	Callinectes similis	–	0.16	–	0.03
	Callinectes spp.	5.39	7.00	4.59	5.57
	Portunus spp.	–	0.04	0.06	–
	Unidentified Portunidae	0.09	2.16	1.27	0.28
	Ovalipes oscellatus	0.27	–	1.02	0.01
	Ovalipes spp.	0.01	0.09	0.04	0.02
	Pagurus pollicaris	0.38	0.09	0.83	0.09
	Unidentified Paguridae	–	0.07	–	0.02
	Menippe spp.	0.01	0.04	0.05	0.01
	Libinia spp.	0.03	0.09	0.54	–
	Ocypode quadrata	–	0.03	0.04	–
	Hepatus epheliticus	0.01	–	–	0.01
	Unidentified Panopeidae	0.03	–	0.02	0.01
	Unidentified Brachyuran	5.41	4.34	21.24	1.10
Shrimp	*Litopenaeus setiferus*	1.46	1.15	7.48	0.49
	Farfantepenaeus aztecus	0.13	–	0.69	–
	Unidentified Penaeidae	8.13	8.88	25.35	3.77
	Palaemonetes spp.	0.01	0.17	0.03	0.05
	Upogebia affinis	–	0.02	–	0.01
	Alpheus spp.	–	0.02	–	0.01
	Unidentified shrimp	0.04	1.46	0.29	0.33
Stomatopods	*Squilla* spp.	0.10	–	0.19	0.01
	Unidentified Squillidae	0.13	0.34	0.89	0.05
	Unidentified Stomatopod	0.11	0.07	0.85	–
Cephalopods	Unidentified Tuethida	0.26	–	0.90	–
Teleost fishes	*Brevoortia* spp.	0.08	0.05	0.70	0.02
	Unidentified teleost	0.95	1.53	4.66	0.30
Other arthropods	*Limulus polyphemus*	0.12	0.03	–	0.15
	Unidentified arthropod	0.28	0.22	1.12	0.01
Macroalgae	Unidentified macroalgae	0.03	0.27	0.35	0.02

netheads from Texas (53.8 %FO), northwestern Florida (66.7 %FO), west–central Florida (77.7 %FO) and eastern Florida (50.0 %FO). Bonnetheads from west central Florida consumed the most seagrasses (16.0 %IRI). Stomatopods, mostly *Squilla* spp., were present in the diet of individuals collected in Texas and west central Florida, although they comprised less than 3 %IRI in both regions. Teleost fishes made up

Fig. 2. % IRI contributions of each major prey group to both male and female bonnetheads (*Sphyrna tiburo*) from South Carolina. Prey groups contributing to < 5 % of diet (cephalopods, macroalgae, and other arthropods) have been combined into 'Other' category.

*Fig. 2. Contribuciones al porcentaje del indicador de importancia relativa (%IRI) de cada grupo de presas a las cornudas de corona (*Sphyrna tiburo*) machos y hembras de Carolina del Sur. Los grupos de presas que representan < 5 % de la dieta (cefalópodos, macroalgas y otros artrópodos) se han agrupado en la categoría "Other".*

1.6 %IRI of immature bonnethead diet in South Carolina. Bonnetheads collected in Texas and northwestern Florida consumed the most macroalgae (1.1 % and 1.5 %IRI, respectively). A notable portion of immature bonnethead diet in eastern Florida was other arthropods (3.3 %IRI), primarily *Limulus polyphemus*. All other diet categories comprised less than 1 %IRI and were considered comparatively insignificant. No immature bonnetheads from Alabama were included in this study due to low sample size (n = 1).

The diet of mature bonnetheads was similar between regions (fig. 1). Texas, South Carolina, and northwestern Florida mature bonnetheads consumed a comparable quantity of crabs (85.9 %, 88.2 %, and 89.5 %IRI); however, the diet of mature sharks in Alabama and eastern Florida was nearly entirely composed of crabs (97.1 % and 97.3 %IRI, respectively). South Carolina was the only region where the adult bonnetheads consumption of shrimp was substantial (9.8 %IRI), predominately penaeid shrimp (table 2). Seagrasses, primarily *Thalassia testudinum* and *Halodule wrightii,* were found in mature bonnetheads from Alabama (11.1 %FO), northwestern Florida (70.0 %FO), west–central Florida (75 %FO), and eastern Florida (12.5 %FO). Bonnetheads from west central Florida consumed the most seagrasses (28.3%IRI) and this was the only region where mature sharks consumed a substantial amount of macroalgae (4.0 %IRI), although individuals in Texas and northwest Florida also consumed macroalgae (2.0 % and 1.3 %IRI, respectively). Stomatopods, largely *Squilla* spp., contributed to diet of bonnetheads in Texas (5.4%IRI) and west central Florida (3.1%IRI; fig. 1). Teleost fishes were a minor contribution in the diet of bonnetheads from Texas, Alabama, northwestern Florida, and South Carolina (2.2 %, 2.4 %, 1.2 %, and 1.0 %IRI, respectively).

Similar to other regions studied, South Carolina bonnethead diet was dominated by crabs, especially in the family Portunidae. However, while shrimp were nearly absent from other regions, they comprised a substantial part of both immature and mature bonnethead diet (fig. 1). No seagrasses were found in the stomachs of South Carolina bonnetheads, nor were macroalgae found to be an important part of their diet (< 0.5 %IRI). Overall, no notable differences in mature and immature diet of South Carolina bonnetheads were observed (fig. 1, table 2). Diet was also compared between male (n = 36) and female (n = 60) bonnetheads in South Carolina to examine potential differences in diet due to sexual segregation. Broadly, female diet was almost entirely composed of crabs whereas males consumed much lower quantities of crabs (94.8 %IRI and 56.5 %IRI, respectively). Female bonnetheads also consumed less shrimp and teleost fishes than males (fig. 2). The species composition of diet varied between males and females. *Callinectes* spp. accounted for the most identified crabs consumed by both sexes, however, they were more abundant in the diet of females than males (93.3 % and 31.3 %IRI, respectively). In male bonnetheads from South Carolina penaeid shrimp composed a larger portion of the diet than *Callinectes* spp. (table 2).

Table 3. Results of statistical analysis comparing %W between the three distinct population structures of bonnetheads (*Sphyrna tiburo*): western Gulf of Mexico (WGOM), eastern Gulf of Mexico (EGOM), and Atlantic (ATL). Each column displays results of one of the three comparisons made. Percentages resulting from SIMPER test indicate contribution of each prey group to dietary differences between regions: Df, degreess of freedom.

*Tabla 3. Resultados del análisis estadístico en el que se compara el porcentaje de peso de tres poblaciones distintas de cornuda de corona (*Sphyrna tiburo*): el golfo de México occidental (WGOM), el golfo de México oriental (EGOM) y el Atlántico (ATL). En cada columna se muestran los resultados de una de las tres comparaciones realizadas. Los porcentajes resultantes del análisis SIMPER indican la contribución de cada grupo de presas a las diferencias de las dietas entre regiones: Df, grados de libertad.*

	WGOM EGOM	EGOM ATL	WGO ATL
PERMANOVA			
Df	1	1	1
F–statistic	21.296	8.079	12.47
p–value	≤ 0.001	≤ 0.001	≤ 0.001
Betadisper ANOVA			
p–value	0.5761	0.9418	0.6435
SIMPER			
Crabs	43.13 %	41.71 %	43.12 %
Stomatopod	20.63 %	13.31 %	15.76 %
Seagrasses	12.40 %	9.90 %	4.03 %
Shrimp	6.71 %	19.56 %	22.50 %
Teleost	6.49 %	6.35 %	5.38 %
Macroalgae	4.10 %	3.14 %	1.04 %
Cephalopod	3.45 %	0.89 %	4.22 %
Other arthropod	3.09 %	5.14 %	3.95 %

Species accumulation curves for each region approached an asymptote, indicating that sufficient samples had been processed from each region to accurately represent the diet (fig. 1s in supplementary material). The PERMANOVA tests found that each regional diet was significantly different from the others (table 3). The subsequent betadisper and ANOVA found that the differences observed by the PERMANOVA were due to location effects (table 3). The SIMPER test found that the primary prey group driving the differences in all comparisons were crabs. Between the western GOM and eastern GOM, the observed difference in %W was driven primarily by crabs, followed by stomatopods and seagrasses. Bonnetheads in the western GOM consumed more crabs and stomatopods, whereas bonnetheads in the eastern GOM consumed more seagrasses. The differences observed both between the western GOM and Atlantic and eastern GOM in the Atlantic were also primarily due to differences in crab consumption, followed by shrimp then stomatopods. Crabs were most prevalent in the diet of western GOM bonnetheads, followed by Atlantic bonnetheads. Shrimp were most prevalent in the diet of bonnetheads from the Atlantic while both GOM regions consumed more stomatopods than the Atlantic (table 3).

Discussion

Overall, bonnethead diet did not vary widely among locations investigated, and was universally dominated by crabs, confirming that crabs are the most important prey in the diet of bonnetheads across their range (Cortés et al., 1996; Lessa and Almeida, 1998; Bethea et al., 2007; Plumlee and Wells, 2016; Kroetz et al., 2017), with a few exceptions (Bethea et al., 2007). This study showed a preference for *Callinectes* spp. by bonnetheads in South Carolina that has been well documented in the GOM (Cortés et al., 1996; Lessa and Almeida, 1998). Bonnetheads in South Carolina consumed a proportion of shrimp that has only been previously observed in Alabama (Kroetz et al., 2017). However, the mature bonnetheads from Alabama in this study had almost no shrimp in their stomachs. Ontogenetic shifts in diet have been observed in bonnetheads in northwestern Florida (Bethea et al., 2007), but not elsewhere in their range (Cortés et al., 1996; Kroetz et al., 2017) and no clear ontogenetic dietary shifts were detected in our study. Regional dietary differences in prey weight detected were due to differences in the relative proportion of secondary prey categories, but the diet of all bonnethead populations was dominated by crabs across the analyzed range.

While immature and mature bonnethead diet in South Carolina was similar, consuming comparable quantities of *Callinectes* spp. and penaeid shrimp, males and females displayed significantly different diets. Females in South Carolina consumed almost exclusively *Callinectes* spp., whereas male bonnetheads had a more diverse diet that included a substantial amount of penaeid shrimp. Previous bonnethead trophic studies found sex–based differences in daily ration in the GOM (Bethea et al., 2007), but no significant dietary differences between females and males in western Florida (Cortés et al., 1996) and northern Brazil (Lessa and Almeida, 1998). Driggers et al. (2014) suggested that female adult bonnetheads in South Carolina feed heavily on *Callinectes* spp. in the estuary to support gestation. Our results support this hypothesis; ovigerous *Callinectes sapidus* migrate from low salinity waters to higher salinity waters near the mouths of estuaries (Carr et al., 2004), and occur in South Carolina estuarine waters April through August, mainly in salinities above 15 ppt (Archambault et al., 1990). However, whether the observed difference in diet is due to female preference for *Callinectes* spp. or is simply a function of each sex occupying different habitats is unclear. Sexual differences in diet have been documented in sharks, yet are not universal, even in sexually segregated sharks (Simpfendorfer et al., 2001; McElroy et al., 2006). Habitat has been suggested to be the most important determinant of bonnethead diet (Cortés et al., 1996), and thus a spatially segregated population of males and females would be expected to have different diets. Previous research documented a 9:1 female to male sex ratio in in South Carolina estuarine waters (Ulrich et al., 2007). While the male bonnetheads examined in this study were captured in estuarine waters, they likely spend most of their time in nearshore coastal waters with lower *Callinectes* spp abundance (Ulrich et al., 2007), therefore stomach contents may be representative of nearshore foraging, or retention of a nearshore preferred prey when moving into estuarine waters.

Bonnetheads have been found to consume seagrasses in substantial quantities where seagrasses exist (Cortés et al., 1996; Bethea et al., 2007; Kroetz et al., 2017), and immature bonnetheads consume more seagrass than adults (Bethea et al., 2007; Kroetz et al., 2017). The results of this study confirm these observations. We found that bonnetheads living in seagrass ecosystems consume seagrasses, with immature sharks ingesting higher proportions of seagrass. The exception in our data was west central Florida, where seagrasses were nearly twice as important in mature bonnethead diet than in juveniles; however, this anomaly is likely an artifact of low sample size of mature fish from this study site (n = 12). Seagrass consumption by sharks is not unique to bonnetheads. Juvenile lemon sharks *Negaprion brevirostris* also ingest seagrasses (Cortés and Gruber, 1990), indicating seagrass consumption may be a relatively common occurrence in sharks that feed in seagrass beds. Bonnetheads feed mostly on benthic prey *Callinectes* spp., further increasing the likelihood of accidentally ingesting seagrasses. Generally, plant material found in shark stomachs has been considered incidental (Cortés and Gruber, 1990; Cortés et al., 1996; Kroetz et al., 2017). Originally, it was considered unlikely that bonnetheads had the digestive enzymes necessary to digest plant matter (Cortés et al., 1996; Bethea et al., 2007). Seagrasses were observed in 11.0 %–77.7 % of bonnethead stomachs that were collected in regions with seagrasses present, but these results do not directly prove that bonnetheads are omnivorous. However, our results support the concept proposed by Leigh et al. (2018) that bonnetheads may play a more substantial role as nutrient vectors in seagrass ecosystems than previously recognized.

Despite the potential benefits of inhabiting seagrass ecosystems, bonnetheads routinely occupy habitats devoid of seagrasses such as the estuaries of South Carolina (Dame et al., 2000; Driggers et al., 2014). Bonnethead diet in South Carolina did not include seagrasses as they are not present in the lowland *Spartina* spp. marsh environments in this region (Green and Short, 2003). The results of this study indicate that seagrass consumption is not a necessary component of bonnethead diet, at least during periods of up to 7–8 months when they occupy areas devoid of seagrasses (Driggers et al., 2014). If plant material is a necessary component of bonnethead diet, individuals in South Carolina could supplement their diet with the available macroalgae, however, almost none was found in stomach contents (0.03 %–0.27 %IRI). It is also possible that bonnetheads could consume seagrasses when they migrate south to the east coast of Florida (Driggers et al., 2014), though this study provides no evidence that this is the case.

In conclusion, our data indicate that bonnethead diet is dominated by crabs, primarily portunids, across the geographical range analyzed, though the relative importance of crabs varied between regions. Bonnetheads in South Carolina have a similar dietary reliance on crabs (especially *Callinectes* spp.) as has been found elsewhere in their range (Cortez et al., 1996; Lessa and Almeida, 1998; Bethea et al., 2007; Plumlee and Wells, 2016; Kroetz et al., 2017), though dietary differences can be found between populations. Diet of bonnetheads in South Carolina include a significant amount of shrimp, to an extent only previously observed in Alabama (Kroetz et al., 2017). Our results also suggest that male and female bonnetheads in South Carolina have different diet, a behavior that has not been observed elsewhere in their range (Cortés et al., 1996; Lessa and Almeida, 1998).

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Supplementary material

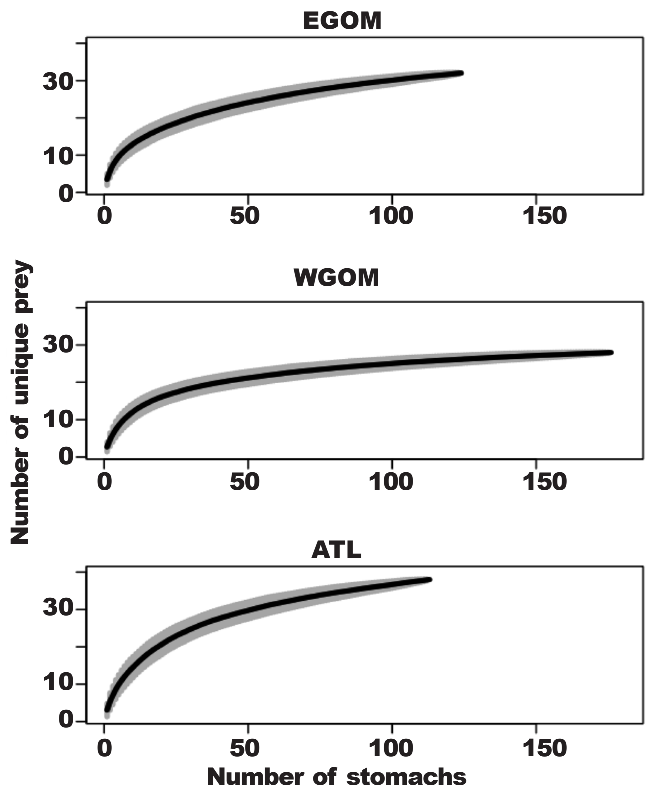

Fig. 1s. Species accumulation curves for the east Gulf of Mexico (EGOM), west Gulf of Mexico (WGOM) and Altantic (ATL) regions. Number of stomachs sampled for each region are plotted against number of unique prey items found in stomachs.

Fig. 1s. Curvas de acumulación de especies en las regiones del golfo de México oriental (EGOM), el golfo de México occidental (WGOM) y el Atlántico (ATL). Se representa el número de estómagos analizados en cada región en relación con el número de presas únicas encontradas en los estómagos.