



Trophic ecology of Carolina *Sphyrna gilberti* and scalloped *S. lewini* hammerheads in the southeastern USA

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ABSTRACT: Carolina hammerheads *Sphyrna gilberti* and scalloped hammerheads *S. lewini* are cryptic species with an overlapping distribution, and young-of-the-year (YOY) use similar coastal and estuarine nursery areas along the US Southeast coast. The diet of scalloped hammerheads has been widely studied throughout their global distribution; however, little is known about their diet in the western North Atlantic Ocean. Carolina hammerheads have only been recently described, and as such, their trophic ecology is largely unstudied. Stomach content analysis of genetically identified YOY Carolina and scalloped hammerheads revealed both species to be generalist feeders with diverse diets and no apparent resource partitioning between them. By contrast, multi-tissue (muscle and plasma) stable isotope analyses showed significant interspecific differences in signatures, particularly in muscle $\delta^{13}\text{C}$ values for the youngest hammerheads. Due to slow tissue turnover rates, YOY muscle signatures were assumed to reflect maternal isotopic signatures, suggesting habitat or resource partitioning between mature female Carolina and scalloped hammerheads. In particular, the data are consistent with mature Carolina hammerheads inhabiting more offshore waters or consuming a higher proportion of pelagic prey relative to scalloped hammerheads. YOY muscle and plasma $\delta^{15}\text{N}$ values decreased drastically across the sampling season, reflecting a loss of the maternal signal as the YOY hammerheads fed and grew rapidly in these productive nursery habitats.

KEY WORDS: Stomach contents · Stable isotope analysis · Elasmobranch · Young-of-year · Nursery habitat · Cryptic species · Maternal provisioning

1. INTRODUCTION

Sympatric species may exhibit different resource use patterns to reduce competition, whether it be ontogenetic changes (i.e. different habitat use or diet

of juveniles and adults), temporal partitioning, or partitioning of resources by individuals within a shared life stage and habitat (Ross 1986, Bethea et al. 2004, Papastamatiou et al. 2006, Kinney et al. 2011, Besnard et al. 2024). Understanding resource use patterns

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such as overlap or partitioning within habitats supporting multiple species, such as nursery areas, or how patterns of intra- and interspecific resource use vary between life stages can lead to better management practices and knowledge of predator–prey dynamics. However, migratory animals such as sharks are difficult to study and therefore resource use patterns may often remain unknown through traditional methods (i.e. tagging or diet studies).

The Carolina hammerhead *Sphyrna gilberti* is a cryptic species that is externally indistinguishable in morphology from the scalloped hammerhead *S. lewini* (Quattro et al. 2006, 2013). While the scalloped hammerhead has a circumglobal distribution, inhabiting temperate and tropical coastal and semi-oceanic waters (Compagno 1984), the Carolina hammerhead has mostly been found in estuarine and nearshore waters off the southeastern USA, with a few individuals reported in Brazil (Pinhal et al. 2012, Barker et al. 2021). Despite extensive sampling, the Carolina hammerhead has not been detected in the Gulf of Mexico (Barker et al. 2021) and their full distribution in the Atlantic is unclear. In the most recent US stock assessment, Carolina hammerheads could not be assessed separately from scalloped hammerheads due to the former's data-deficient status. With species combined, the Atlantic population was determined not to be overfished with no overfishing occurring (SEDAR 2023). However, given their limited distribution, Carolina hammerheads may be more vulnerable to anthropogenic pressures than scalloped hammerheads. Furthermore, hybridization has been detected between the rarer Carolina and more common scalloped hammerhead (Barker et al. 2019), with most backcrosses involving scalloped hammerheads, suggesting that genetic swamping may be a concern. Finally, there is a lack of important biological information pertaining to the Carolina hammerhead's life history and ecology. The fact that the 2 species can only be differentiated retrospectively through genetic testing (or through precaudal vertebral counts, necessitating lethal sampling) represents a challenge for filling outstanding data gaps needed to assess and/or manage the species independently of the scalloped hammerhead.

Most biological information on Carolina hammerheads to date has been gathered during their early life history. As is the case for many coastal shark species, both Carolina and scalloped hammerheads rely on estuarine and coastal habitats as nursery areas during their first years of life (Clarke 1971, Castro 1993, Adams & Paperno 2007, Ulrich et al. 2007, Barker et al. 2021), making them easily acces-

sible to researchers at these early life stages. By contrast, adults of both species are more difficult and costly to study using traditional methods, making it challenging to characterize adult movement patterns and feeding habits. Young-of-the-year (YOY) hammerheads, which are reliably collected in nursery grounds, can be used to provide insights into the species' ecology on the nursery grounds as well as the potential for niche overlap between the 2 species. Functionally similar species may exhibit niche partitioning (e.g. dietary, spatial, or temporal partitioning) to reduce competition (Kinney et al. 2011, Matich et al. 2017), and effective management requires an understanding of the foraging and spatial dynamics of co-occurring species. While Carolina and scalloped hammerheads coexist across multiple nursery areas along the southeastern US coast, the highest proportion of YOY Carolina hammerheads was found in Bulls Bay, South Carolina, an important nursery for both species (Castro 1993), delineating this region as the primary known nursery ground for the species (Barker et al. 2021). Growth studies on YOY hammerheads suggest that both species rely on these nursery habitats for abundant food resources to quickly replenish lost energy reserves and increase size (Lyons et al. 2020).

Methods for examining feeding ecology (i.e. stomach contents and stable isotopes) can be applied to explore how these animals may be partitioning shared resources. Stomach content analysis is a traditional method used to assess diet, which can provide specific taxonomic resolution of prey items and a quantitative assessment of feeding habits. Dietary studies have increasingly used stable isotope analysis (SIA) as a complementary approach to study species ecology because it provides tissue-specific, time-integrated data about a predator's assimilated diet while also being cost-effective and often non-lethal. Carbon isotopic values (as represented by $\delta^{13}\text{C}$) can broadly track animal movements and infer foraging location through the basal carbon source (e.g. benthic or coastal vs. pelagic or offshore food webs) since they vary between primary producers but remain relatively constant between prey and predator, while nitrogen isotopic values ($\delta^{15}\text{N}$) infer the relative trophic position of an organism, as they increase in a stepwise manner from prey to predator (Peterson & Fry 1987, Post 2002). Adding a third tracer, sulfur ($\delta^{34}\text{S}$), can further distinguish benthic from pelagic feeding habits, especially in estuaries where organic matter sources are numerous and mixed (Peterson & Fry 1987, Hussey et al. 2012). Combining these analyses provides a comprehensive understanding of a par-

ticular species' trophic role in an ecosystem over short and long time scales, including habitat use and preference, foraging success, and resource overlap or partitioning among sympatric species (Domi et al. 2005, Hussey et al. 2011, Shaw et al. 2016, Kroetz et al. 2017, Young et al. 2018).

Interpreting stable isotope signatures from the youngest sharks can be difficult due to maternal influence on YOY tissues, especially in placental sharks like hammerheads due to maternal provisioning (Lyons et al. 2020). In young sharks, tissue $\delta^{15}\text{N}$ values can be higher relative to their mother (Olin et al. 2011) and $\delta^{13}\text{C}$ may reflect the carbon source of maternal prey rather than YOY prey. Although the maternal signal fades as young sharks grow, the length of time required to 'wash out' this signal varies with tissue turnover rate. Muscle tissue has one of the longer turnover rates, making SIA in this tissue more challenging to interpret since maternal signatures persist for months to years after birth in young sharks (Olin et al. 2011, Niella et al. 2021). By contrast, tissues with faster turnover rates (such as plasma; Tieszen et al. 1983, Logan & Lutcavage 2010, Kim et al. 2012, Caut et al. 2013) can be used to interpret the ecology of YOY individuals with more confidence. Performed in tandem, stomach contents can be used to ground-truth results of fast turnover tissues, while inferences about trophic or spatial differences in food resources for mature females can be made using slow turnover tissues from YOY individuals. Employing this approach provides an avenue for studying the ecology of adult female Carolina and scalloped hammerheads without having to catch them, which is particularly useful since adult female Carolina hammerheads have not been encountered to date.

The purpose of this study was to investigate the trophic ecology of YOY Carolina and scalloped hammerheads in nursery grounds along the southeastern US coast (South Carolina, Georgia, and eastern Florida). The objectives of the research were to (1) describe and compare the diet of sympatric YOY hammerheads across 3 states, with a focus on Bulls Bay, South Carolina, by analyzing stomach contents in tandem with plasma isotopic signatures, and (2) make inferences about the trophic ecology of mature female hammerheads by leveraging maternal isotopic signatures in YOY muscle. These data will fill information gaps pertaining to adult Carolina and scalloped hammerheads while providing critical information about how these young animals use nearshore nursery grounds, which will be valuable for the conservation and management of habitat essential for both species.

2. MATERIALS AND METHODS

2.1. Sample collection

YOY hammerheads were collected from multiple nurseries and nearshore waters along the southeastern US coast between April and October from 2014 to 2019, with most samples collected in Bulls Bay, South Carolina (Fig. 1). Hammerheads were primarily collected through fishery-independent surveys using gillnets and bottom longlines, and opportunistically as bycatch from commercial and fishery-independent trawls. Fork length was measured to the nearest mm, and sex and umbilical scar stage (USS) were determined for all sharks. USS is the best proxy for time since birth due to variable lengths-at-birth and parturition periods for both species (Lyons et al. 2020). Umbilical scars were characterized by varying stages of healing in a similar fashion to Duncan & Holland (2006) as follows: USS1 (unhealed or partially healed), USS2 (well healed), USS3 (fully healed, no scar present).

Fin clips were taken from the free rear tip of the first dorsal fin, stored in salt-saturated 20% dimethyl sulfoxide buffer (Seutin et al. 1991), and sent to the Marine Genomics Laboratory at Texas A&M University—Corpus Christi, where species were identified genetically by using double-digest restriction associated DNA sequencing to characterize diagnostic single-nucleotide polymorphisms that are fixed between hammerhead species (Barker et al. 2019). Samples were then retrospectively assigned as either Carolina hammerhead, scalloped hammerhead, or hybrid (mixed parentage). Hybrids most often occur through sex-biased gene flow from mating events between a female Carolina hammerhead and a male scalloped hammerhead (Barker et al. 2019). Because of their limited numbers, hybrids were considered separately in all subsequent analyses.

Upon capture, blood was taken as soon as possible via caudal venipuncture and collected in non-heparinized vacutainers to be processed later in the day. In the laboratory, blood was centrifuged at $1900 \times g$ (4000 rpm) for 5 min to separate layers, and the plasma was aspirated from the red blood cell pellet prior to freezing. At necropsy, the stomach was extracted, and the contents were excised and stored in a bag to reduce further digestion. Muscle samples were taken from the dorsal musculature near the base of the dorsal fin. All samples were frozen (-20° or -80°C) until analysis.

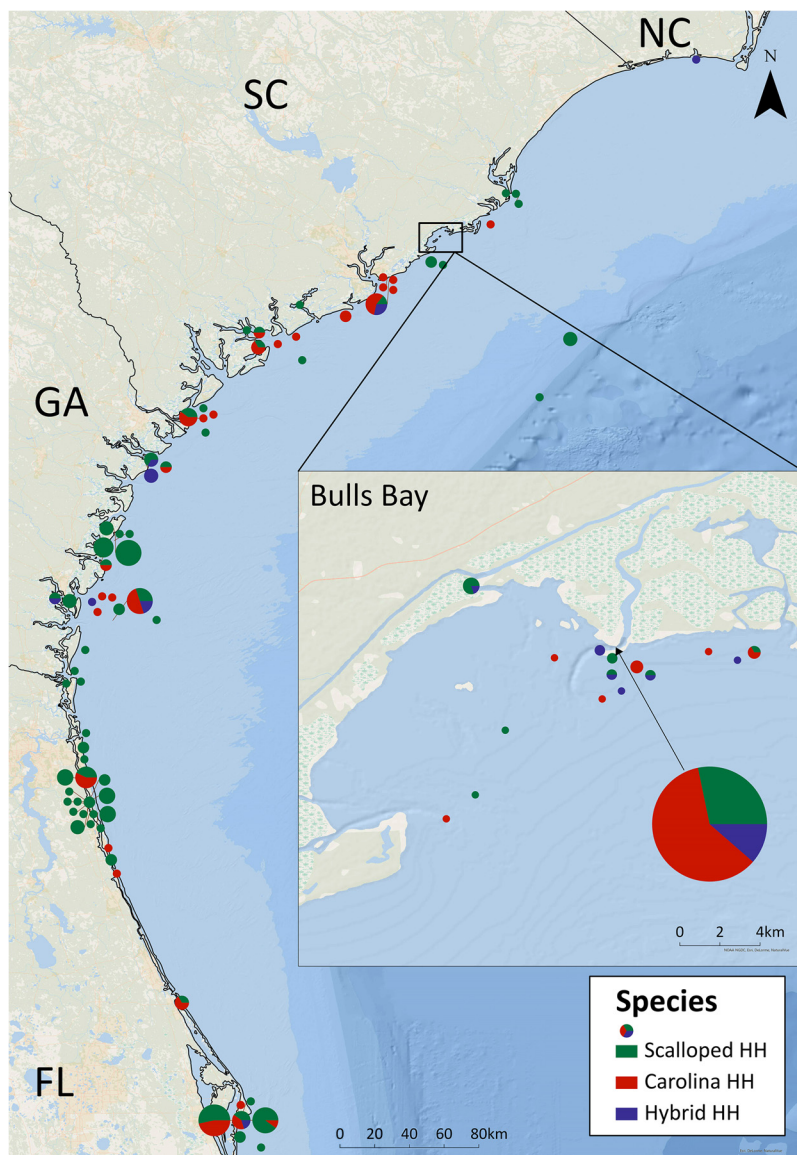


Fig. 1. Sample locations in the western North Atlantic Ocean along the southeastern US coast (NC, North Carolina; SC, South Carolina; GA, Georgia; FL, Florida), with proportions of hammerhead (HH) species denoted by color. Circle size is proportional to sample size, with larger circles indicating more samples from that location

2.2. Stomach content analysis

Stomach contents were thawed and prey items from each specimen were rinsed through a sieve, then sorted, enumerated, weighed (wet weight to the nearest 0.001 g), and identified to the lowest possible taxonomic resolution. A general digestion code (DC) was assigned to each prey item: (1) relatively fresh prey with full or partial skin or carapace, often mostly whole or cleanly bitten; (2) large pieces of flesh with bones (no skin) for teleosts, large pieces of shrimp

without carapace or intact mantle or tentacles for squid; (3) vertebrae and bones with no tissue, or pieces of tissue without bones for teleosts, small parts of shrimp (i.e. rostrum, legs and gills only), small pieces of tentacles and/or pen for squid; or (4) hard parts only (i.e. otoliths, eye lenses, squid beaks or very digested small pieces of shrimp carapace or legs).

Prey species accumulation curves were used to determine if a sufficient number of stomachs were collected for a comprehensive description of Carolina and scalloped hammerhead diet in Bulls Bay. Curves were created using the package 'vegan' v.2.6.4 (Oksanen et al. 2002) in R (R Core Team 2023) with 1000 permutations and subsampling without replacement (Gotelli & Colwell 2001). Chao's diversity estimator (Chao 1987, Chiu et al. 2014) was calculated to estimate if more unique prey species could be uncovered in the diet with further sampling.

To reduce biases related to variable levels of prey identification (due to different states of digestion), all diet indices were calculated using 7 prey taxonomic categories: Engraulidae, Sciaenidae, other teleosts, unidentified teleosts, shrimps, other crustaceans, and molluscs. Relative measures of each prey category were quantified by calculating the percent frequency of occurrence (%O), percent composition by number (%N), percent composition by weight (%W) (Hyslop 1980), and percent index of relative importance (%IRI; Cortes 1999). Measures of variance, mean percent number (%MN) and mean percent weight (%MW) for a prey category were calculated by averaging the value of %N and %W across all individual stomachs (Ferry & Cailliet 1996, Chipps & Garvey 2007), which were used with %O to calculate the mean %IRI (%IRI_M). This method reduces bias and enables the calculation of variances around each metric for statistical comparison (Chipps & Garvey 2007). All relative measures described above were also calculated for each prey item in Bulls Bay hammerheads and across the sampling region and are included in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m743p025_supp.pdf.

Prey diversity was compared between the hammerhead species in Bulls Bay using a 2-sample *t*-test for 2 indices of diversity: Shannon index and species richness. Multivariate variance analyses (ANOSIM and PERMANOVA with 999 and 9999 permutations, respectively) were conducted to assess differences in diet between species using square-root transformed %N data of the 7 prey categories, which was then compiled into a Bray-Curtis dissimilarity matrix. ANOSIM was also conducted using %W for comparison to other studies. For PERMANOVA results, a 'betadisper' analysis was first used to test homogeneity of multivariate dispersions and determine whether the PERMANOVA results were due to dispersion (variability of dietary composition within groups) or location (dietary composition difference between groups) effects. A significant betadisper *p*-value of <0.05 indicates a difference in dispersion and, potentially, species, while a non-significant *p*-value indicates a species difference. A SIMPER analysis was conducted to determine which prey items explained any dissimilarity between variables. All multivariate analyses were conducted using 'vegan'. Statistical significance was declared at *p* < 0.05.

Dietary niche overlap between species was assessed by calculating Pianka's overlap index (Pianka 1976) using %MN and %MW of prey categories. Pianka's overlap indices were calculated with a null model (EcoSimR; Gotelli et al. 2015). An observed value greater than the simulation index suggests either an absence of competition between species or that competition exists but has yet to lead to partitioning of resources (Bethea et al. 2007). The RA3 algorithm was used to generate a distribution of expected overlap values generated from 1000 repetitions of the diet data. High overlap values (≥ 0.6) are considered biologically significant (Zaret & Rand 1971, Pianka 1976) and suggest large resource overlap, while low values suggest different diets or partitioning of resources (Gotelli & Graves 1996).

If no differences in diet composition were found between species within Bulls Bay, species were combined to examine temporal differences in Bulls Bay by comparing %IRI of prey categories by month of capture. Due to limited sample sizes outside of Bulls Bay, potential latitudinal differences were qualitatively explored by visually comparing stomach content metrics across states (i.e. South Carolina, Georgia, and eastern Florida).

2.3. SIA

Muscle and plasma samples were lyophilized, homogenized, and packed into 4 × 6 mm tin capsules

for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic analyses, with a subset of muscle samples also analyzed for $\delta^{34}\text{S}$. Prior to this analysis, muscle tissue was extracted following a modified Bligh & Dyer (1959) method for lipid extraction and rinsed with deionized water to remove urea. Lipids and urea were removed from muscle because lipids are depleted in ^{13}C relative to protein and ^{14}N is preferentially concentrated in urea, thus causing the carbon and nitrogen isotopic signatures to be more depleted, which can bias interpretation (Kim & Koch 2012, Carlisle et al. 2017). All C:N ratios of extracted muscle and plasma samples were below 3.5, and no mathematical normalization corrections were applied (Post et al. 2007).

A subset of extracted muscle samples was also analyzed for $\delta^{34}\text{S}$ to further delineate potential differences in Carolina and scalloped hammerhead maternal baselines (i.e. benthic versus pelagic). As estuaries are highly mixed, interpreting possible resource partitioning can be difficult with $\delta^{13}\text{C}$ alone. However, combining $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ can be used to more confidently determine whether prey resources are derived from benthic versus pelagic food webs.

All stable isotopes were analyzed at the University of California Davis Stable Isotope Facility. Muscle and plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon), while muscle $\delta^{34}\text{S}$ was measured with an Elementar vario ISOTOPE cube interfaced to an Isoprime PrecisiON IRMS (Cheadle Hume). Stable isotopes are expressed in delta notation (‰) as differences from a standard (R_{standard}): $\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where *X* is ^{15}N , ^{13}C , or ^{34}S and R_{sample} refers to the ratio of heavy isotope to light isotope ($^{13}\text{C}:^{12}\text{C}$, $^{15}\text{N}:^{14}\text{N}$, $\text{S}^{34}:\text{S}^{32}$). Final isotope values are expressed relative to international standards Vienna Pee Dee Belemnite for carbon, atmospheric nitrogen, and Vienna Canyon Diablo Troilite for sulfur. The mean standard deviations for reference material replicates were <0.07‰ for $\delta^{13}\text{C}$, $\leq 0.1\%$ for $\delta^{15}\text{N}$, and 0.4‰ for $\delta^{34}\text{S}$.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were individually compared between species by tissue (muscle or plasma) in Bulls Bay using Wilcoxon rank sum tests. Within Bulls Bay, differences by month, USS, or year were assessed per species using non-parametric Kruskal-Wallis *H*-tests. If significant differences were found, pairwise comparisons were conducted with a Dunn's test adjusted with the Benjamini-Hochberg false discovery rate procedure. To explore interspecific maternal differences, a Wilcoxon rank sum test was performed with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on the youngest hammerheads (i.e.

those with unhealed umbilical scars and the highest amount of maternal influence) by tissue.

Quantitative metrics to assess isotopic comparisons were calculated according to Layman et al. (2007), which include the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range between the most and least enriched individuals within a group, the total area (TA) or the convex hull area encompassed by all individuals in a group on an isotopic bi-plot, and mean distance to the centroid, which represents the average degree of diversity within a species. The standard ellipse area corrected for small sample size (SEAc), which represents the core niche area (isotopic niche) of each species or subgroup and comprises approximately 40% of the isotopic data, was calculated to compare isotopic niches of each species and subgroup. Overlap of the standard ellipses was calculated to represent the degree of shared isotopic niche space between groups, and values of >60% were considered biologically significant (Guzzo et al. 2013, Dance et al. 2018). Metrics and ellipse overlap were calculated with the SIBER package (Jackson et al. 2011) in R and only using samples from Bulls Bay due to smaller sample sizes from different states and latitudinal isotopic variation along the southeastern US coast (Ceriani et al. 2014). Kernel utilization density estimators (KUDs) were calculated using the 'rKIN' package (Eckrich et al. 2020) (with 40% estimated utilization distribution for comparison to SEAc) to measure isotopic niche size and overlap. KUDs can more accurately estimate niche space (kernel isotopic niche) and overlap with irregularly distributed data and extreme values (Eckrich et al. 2020), and KUD values were compared to those calculated with standard ellipses.

Maternal signal loss was explored by generating SEAc for USS and month of capture by species and tissue. Latitudinal differences were explored with standard ellipse overlap between states (i.e. South Carolina, Georgia, and Florida). To further examine isotopic differences between interspecific feeding habits and between YOY (late summer) and mature female habitat (as inferred from sharks caught in early spring), $\delta^{34}\text{S}$ was plotted against $\delta^{13}\text{C}$. If $\delta^{13}\text{C}$ values are similar between species but $\delta^{34}\text{S}$ varies, then it can be more confidently concluded that species or age classes are feeding from different baselines. $\delta^{34}\text{S}$ values were also compared by species and sampling period (early or late) using a 2-way ANOVA in R Studio (Version 4.3.2).

2.4. Hybrids

Stomach contents analysis metrics were qualitatively compared between hybrids and each species.

Likewise, stable isotope differences between hybrids and each species were quantitatively compared using Kruskal-Wallis *H*-tests. If significant differences were found, then pairwise comparisons with Dunn's test adjusted with the Benjamini-Hochberg false discovery rate procedure (Benjamini & Hochberg 1995) were conducted. Niche overlap using SEAc and KUDs was calculated between hybrids and each species' isotopic signatures. Statistical analyses were performed in R Studio (Version 4.3.2).

3. RESULTS

3.1. Sample distribution

Due to yearly and seasonal differences in abundance between Carolina and scalloped hammerheads in Bulls Bay (Barker et al. 2021) along with differences in directed versus opportunistic sampling effort, sample sizes were not even across years, USS, or months for each state (Table 1, Table S3). A total of 436 stomachs were collected from YOY ($n = 427$) and 1 yr old ($n = 9$) hammerheads, with the majority captured in Bulls Bay (61.8%), followed by Florida (19.2%) and Georgia (14.5%; Fig. 1, Table 1). Species sampling was fairly even between scalloped (43%) and Carolina hammerhead (46%), with hybrids comprising a relatively small portion of samples (~11%). Over half ($n = 244$; 57%) of stomach samples had associated plasma and/or muscle samples taken for SIA. Muscle $\delta^{34}\text{S}$ was analyzed on a subset of YOYs ($n = 36$). Most hybrid stomach (73.9%) and stable isotope (85%) samples were collected from Bull Bay, despite hybrids being detected throughout the southeastern USA (Table 1). In addition, paired tissue samples were collected from older juveniles or mature scalloped hammerheads ($n = 8$) and 1 mature male Carolina hammerhead off the coast of South Carolina (Table S4). The isotopic signatures from these additional samples were only used to place YOY values in context relative to older sharks, the latter of which was excluded from most analyses due to small sample size.

3.2. Stomach content analysis

The digestion status of stomach contents varied between hammerhead species and even within individual stomachs. Most Carolina hammerhead prey items were partially digested (DC 2 and 3, $n = 153$ and 128, respectively, out of 384 total prey items) while most scalloped hammerhead prey items were in an

Table 1. Stomach content analysis (SCA) and stable isotope analysis (SIA) sample sizes by hammerhead species (Carolina *Sphyrna gilberti*, scalloped *S. lewini*, or hybrid) and general location in the southeastern USA: North Carolina (NC), South Carolina (SC), Georgia (GA), and Florida (FL). Locations or nursery areas within a state are denoted by name in parentheses. Paired samples refer to the number of individuals analyzed for both stomach content and stable isotopes. YOY: young-of-the-year; 1 yr: 1 yr old; other: combined mature and older juvenile hammerheads

Group	Location	Paired	SCA		SIA				
			(no. stomachs)		$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$		$\delta^{34}\text{S}$		
			YOY	1 yr	Muscle YOY	Other	Plasma YOY	Other	Muscle YOY
Carolina HH	Combined	100	197	4	97	1	71	1	17
	SC (Bulls Bay)	71	149	3	68		61		9
	SC (nearshore)	9	16		9	1	8	1	2
	GA (nearshore)	5	13	1	5				2
	FL (Cape Canaveral)	9	11		9				4
	FL (nearshore)	6	8		6		2		
Scalloped HH	Combined	123	184	5	118	8	76	8	18
	SC (Bulls Bay)	56	78		56		56		10
	SC (nearshore)	9	8	1	8	4	8	4	1
	SC (offshore)					4		4	
	GA (nearshore)	24	37	3	23		2		
	FL (Cape Canaveral)	11	22	1	10				7
	FL (Tolomato River)	11	22		10		7		
	FL (nearshore)	12	17		11		3		
Hybrid HH	Combined	21	46		20		18		1
	SC (Bulls Bay)	18	34		17		17		
	SC (nearshore)	0	2		1		1		
	GA (nearshore)	1	8		1				1
	FL (Cape Canaveral)	1	1		1				
	NC nearshore		1						
Grand total		244	427	9	235	9	165	9	36

advanced state of digestion (DC 3 and 4, $n = 70$ and $n = 135$, respectively, out of 269 total prey items). Although often only hard parts remained, there were stomachs with multiple fresh whole fish, causing the prey weights to be highly variable between stomachs for comparison. Therefore, all analyses comparing diet were conducted with abundance indices (%N). Scalloped hammerhead prey accumulation curves reached an asymptote, indicating that the number of stomachs sufficiently described the diet (Fig. S1, Table S5), while there was potential under-sampling of Carolina hammerhead stomachs (Fig. S1, Table S5). Nevertheless, since the accumulation curve for Carolina hammerhead was close to an asymptote, it is likely that interspecific comparisons were accurate, particularly when assessed by prey category.

Carolina and scalloped hammerheads appeared to feed continually, since most stomachs were relatively full, contained multiple prey items per stomach, and contained prey at varied stages of digestion (Table S5). Over half of all hammerhead stomachs from Bulls Bay ($n = 230$; 61 scalloped and 64 Carolina hammerhead) had 4 or more prey items (Table S5). Prey species rich-

ness and diversity were higher in scalloped hammerheads than in Carolina hammerheads (Welch $t_{154} = -4.53$, $p < 0.001$ and $t_{185} = -3.96$, $p < 0.001$), with a higher average number of prey items per stomach (6.25 ± 3.4) compared to Carolina hammerheads (3.5 ± 1.9). Though the loss of stomach contents due to regurgitation can be high (Bowen 1996), the proportion of empty stomachs was low ($n = 6$, 2.6%; Carolina $n = 5$ and scalloped hammerhead $n = 1$, respectively; Table S5), and these individuals were excluded from further diet analyses. Three out of 6 empty stomachs were from hammerheads with unhealed umbilical scars (USS1).

Hammerhead diet along the southeast US coast was diverse, with numerous stomachs containing items from 2 or more prey categories (Table S5). The diet of both species combined throughout the sampling region had a wide variety of prey items with at least 32 prey species across 17 identified families of teleosts, crustaceans, and molluscs (Table S2). Out of the 7 prey categories, sciaenids, shrimp, and unidentified teleosts were the 3 most important prey categories for all hammerheads, followed by engraulids and a much

Table 2. Percent mean (\pm SE) number and weight (%MN and %MW, respectively), frequency of occurrence (%O) and mean percent index of relative importance (%IRI_M) calculated for the 7 prey categories of Carolina, scalloped, and hybrid hammerheads in Bulls Bay, SC

Prey taxon	%MN	%MW	%O	%IRI _M
Engraulidae				
Carolina	6.22 \pm 1.33	4.95 \pm 1.48	18.37	1.94
Scalloped	11.76 \pm 2.39	9.86 \pm 2.72	35.06	6.70
Hybrid	2.09 \pm 1.01	2.10 \pm 1.84	12.50	0.42
Sciaenidae				
Carolina	24.45 \pm 2.40	32.40 \pm 3.24	55.10	29.60
Scalloped	27.11 \pm 1.24	30.35 \pm 4.48	59.74	31.14
Hybrid	32.96 \pm 5.13	36.45 \pm 6.58	71.88	39.86
Other teleosts				
Carolina	3.40 \pm 0.88	4.20 \pm 1.35	11.56	0.83
Scalloped	1.25 \pm 1.50	4.37 \pm 1.96	9.09	0.44
Hybrid	2.80 \pm 1.33	4.15 \pm 2.77	12.50	0.69
Unidentified teleosts				
Carolina	34.15 \pm 2.73	27.43 \pm 3.14	63.95	37.21
Scalloped	35.62 \pm 0.50	14.80 \pm 3.14	70.13	32.35
Hybrid	25.48 \pm 4.82	9.42 \pm 3.94	56.25	15.69
Shrimps				
Carolina	22.88 \pm 2.08	27.62 \pm 2.94	59.86	28.56
Scalloped	14.04 \pm 3.19	33.88 \pm 4.28	59.74	25.97
Hybrid	26.92 \pm 3.53	40.86 \pm 6.44	75.00	40.62
Other crustaceans				
Carolina	3.16 \pm 0.99	1.32 \pm 0.73	9.52	0.40
Scalloped	4.31 \pm 1.64	4.89 \pm 2.01	18.18	1.53
Hybrid	4.71 \pm 1.97	2.99 \pm 2.28	18.75	1.15
Molluscs				
Carolina	5.75 \pm 1.04	2.08 \pm 0.77	19.73	1.46
Scalloped	5.90 \pm 3.24	1.84 \pm 0.78	28.57	1.88
Hybrid	4.98 \pm 2.04	4.04 \pm 2.16	21.88	1.58

smaller abundance of molluscs (Table 2, Fig. 2). Sciaenidae was by far the most abundant teleost family, with star drum *Stellifer lanceolatus* as the most commonly identified prey species for both Carolina (%O: 34.9) and scalloped hammerheads (47.3%; Table S2).

Within Bulls Bay, no dietary differences were found between hammerhead species (ANOSIM, $p = 0.81$ and $p = 0.34$ with %N and %W of prey categories, respectively; Table 3, Fig. 2A). Results were similar when unidentified teleosts were removed from the analysis. Dietary composition in Bulls Bay was similar to the diet across the southeastern USA, in which sciaenids, particularly star drum, and penaeid shrimp were dominant prey for both Carolina and scalloped hammerheads (Table S1). This was corroborated by Pianka's overlap index, which suggested a large dietary niche overlap (>0.95) between hammerhead species within Bulls Bay (Table 4). However, with species combined, Pianka's niche overlap values varied across months, in which about half of the combinations had biologically

significant overlap (Table 4). In assessing Pianka's niche overlap with comparison to a null model, the observed overlap values were always higher than the simulated values for all combinations. Dietary composition within Bulls Bay changed by month ($p \leq 0.001$ for both multivariate analyses; Table 3), and this was corroborated by betadisper analysis that indicated potential dietary differences among months and not between species ($F_{2,252} = 1.43$, $p = 0.26$). According to the SIMPER analysis (aside from unidentified teleosts), sciaenids, shrimp, and engraulids contributed the most to dietary differences across months by prey category (Table S6). Sciaenids were more important to hammerheads sampled in July and August, while engraulids were ranked higher in May and June, compared to the other months (Fig. 2B).

Proportions of prey by DC in stomachs across the sampling region were similar to those in Bulls Bay, in which Carolina hammerheads had the highest number of prey items with DC 2 and 3 (37.7 and 33.0%, respectively), while scalloped hammerheads had more prey items with DC 3 and 4 (29.35 and 44.9%, respectively). There was a small proportion of empty stomachs across all states ($n = 16$, 3.7% empty out of

436 analyzed; South Carolina: $n = 9$, 3.1%; Georgia: $n = 2$, 1.6%; and Florida: $n = 5$, 6.1%; Table S5). There was variation in the proportion of the 7 prey categories across states (Fig. S2B) and species when all states were combined (Fig. S2A, Table S1). Sciaenids seemed to be more important to Georgia hammerheads compared to other states, which was likely driven by a much higher %IRI_M of star drum (51.36%) compared to South Carolina (20.75%) and Florida (8.44%) hammerheads. Identifiable teleost species differed with region, with hogchokers *Trinectes maculatus*, gafftopsail catfish *Bagre marinus*, and fringed flounder *Etropus crossotus* only found outside of South Carolina, while 5 sciaenids (banded drum *Larimus fasciatus*, silver perch *Bairdiella chrysoura*, silver seatrout *Cynoscion nothus*, spotted seatrout *C. nebulosus*, and southern kingfish *Menticirrhus americanus*), pinfish *Lagodon rhomboides*, and Atlantic cutlassfish *Trichiurus lepturus* were found in diets of only South Carolina hammerheads. The %IRI_M values for

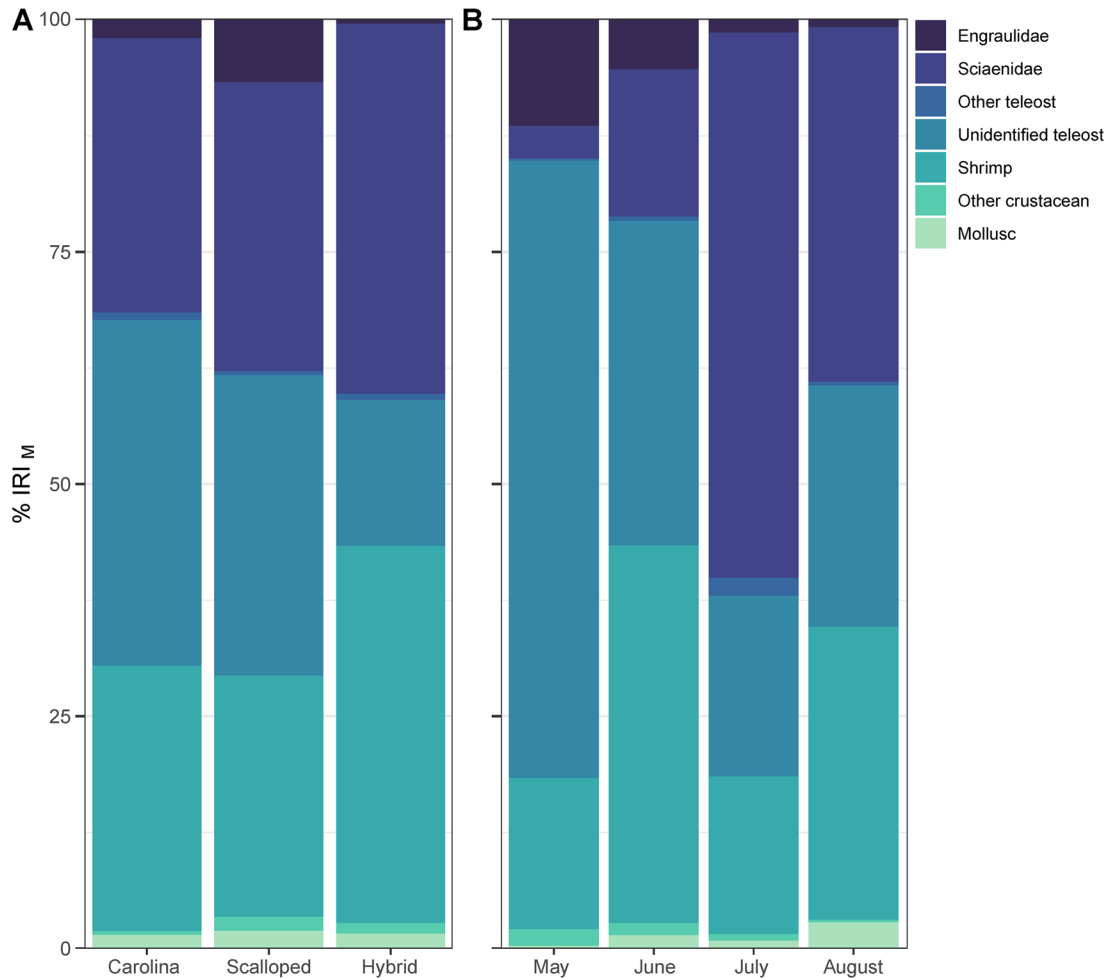


Fig. 2. Percent mean index of relative importance (% IRI_M) of prey categories in Bulls Bay, South Carolina by (A) species (Carolina, scalloped, or hybrid hammerhead) and (B) month of capture (with all hammerheads combined due to similar diet)

prey categories are generally similar between species, except for sciaenids and unidentified teleosts, in which sciaenids have a larger importance in scalloped than Carolina hammerheads (Fig. S2A). Pianka's overlap index indicated there was a large dietary niche overlap (>0.93) between species across all regions. A large overlap was also found between states

with hammerhead species combined (all values >0.84 ; Table 4). Diet diversity varied by state (ANOVA $F_{2,432} = 11.66$, $p < 0.001$), with Florida hammerheads having significantly lower diet diversity (mean \pm SD, $H = 0.55 \pm 0.50$) than either South Carolina or Georgia, which were not different from each other ($H = 0.85 \pm 0.51$ and 0.83 ± 0.50 , respectively).

Table 3. Multivariate analyses using 7 prey categories to compare dietary composition between groups. PERMANOVA was conducted with 9999 permutations and ANOSIM with 999. PERMANOVA was calculated with percent composition by number (%N), while ANOSIM was performed with both %N and percent composition by weight (%W). HH group: comparison of Carolina, scalloped, and hybrid hammerheads, while Species only compared Carolina and scalloped hammerheads

Region	Variable	PERMANOVA				Betadisper		ANOSIM			
		%N				%N		%N		%W	
		df	pseudo- F	p	r^2	F	p	r^2	p	r^2	p
Bulls Bay	Species	1,222	2.34	0.09	0.01	3.65	0.07	-0.018	0.81	0.006	0.34
	HH group	2,253	2.39	0.04	0.02	3.35	0.04	-0.024	0.86	-0.014	0.78
	Month	3,252	9.39	<0.001	0.10	1.43	0.26	0.093	0.001	0.095	0.001

Table 4. Overlap values for stomach contents (Pianka's overlap indices) and stable isotope analysis (standard ellipse area calculated for small sample size [SEAc] and Kernel utilization density estimators [KUDs] calculated with 40% estimated utilization distribution). Overlap indices for stomach content analysis were calculated with mean percent number (%MN) and mean percent weight (%MW). SEAc is the area of overlap in isotopic niche space, with the proportion that overlap comprises for each comparison listed in parentheses (e.g. for plasma within Bulls Bay, species overlap comprised 83% of the Carolina hammerhead ellipse and 66% of the scalloped hammerhead ellipse). The paired values for KUDs should be read the same way as those in parentheses for SEAc. Too few samples from Georgia (GA) precluded its ability to be compared to South Carolina (SC) and Florida (FL)

Region	Comparison	Pianka				SEAc		KUD	
		%MN	p	%MW	p	Muscle	Plasma	Muscle	Plasma
Bulls Bay	Carolina vs. scalloped	0.97	0.001	0.95	0.005	0.00 (0.00, 0.00)	1.51 (0.83, 0.66)	0.00, 0.00	0.38, 0.26
	Carolina vs. hybrid	0.96	0.027	0.91	0.016	0.55 (0.55, 0.59)	1.02 (0.56, 0.79)	0.13, 0.12	0.36, 0.59
	Scalloped vs. hybrid	0.91	0.034	0.97	0.003	0.24 (0.18, 0.26)	1.12 (0.49, 0.87)	0.06, 0.08	0.24, 0.57
	May vs. June	0.92	0.009	0.84	0.072	1.10 (0.81, 0.67)	0.12 (0.10, 0.08)	0.42, 0.63	0.16, 0.18
	May vs. July	0.65	0.214	0.62	0.258	0.01 (0.01, 0.01)	0.00 (0.00, 0.00)	0.06, 0.13	0.00, 0.00
	May vs. August	0.73	0.140	0.79	0.112	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00, 0.00	0.00, 0.00
	June vs. July	0.85	0.091	0.81	0.117	0.31 (0.19, 0.43)	0.05 (0.04, 0.06)	0.10, 0.14	0.06, 0.07
	June vs. August	0.93	0.014	0.90	0.020	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00, 0.00	0.00, 0.00
July vs. August	0.96	0.002	0.97	0.004	0.21 (0.28, 0.29)	0.35 (0.37, 0.83)	0.45, 0.45	0.38, 0.84	
All	SC vs. GA	0.97	0.004	0.94	0.001	0.89 (0.41, 0.56)	—	0.18, 0.24	—
	SC vs. FL	0.95	0.003	0.94	0.016	1.25 (0.58, 0.52)	0.85 (0.37, 0.35)	0.45, 0.24	0.00, 0.00
	GA vs. FL	0.89	0.039	0.84	0.048	1.37 (0.87, 0.58)	—	0.82, 0.51	—

3.3. SIA

3.3.1. Plasma

Overall, there were no interspecific differences in plasma $\delta^{15}\text{N}$ values ($W = 1699$, $p = 0.96$), but $\delta^{13}\text{C}$ values varied slightly ($W = 2095$, $p = 0.03$; Fig. S3A). However, assessment of only the youngest individuals (USS1) revealed Carolina hammerheads having significantly higher $\delta^{15}\text{N}$ values than scalloped hammerheads ($W = 77$, $p < 0.01$), but similar $\delta^{13}\text{C}$ values ($W = 47$, $p = 0.91$). Carolina and scalloped hammerheads showed a similar pattern of less variation in $\delta^{13}\text{C}$ values but large variation in $\delta^{15}\text{N}$ with all samples combined across time (Fig. S3A, Table 5), albeit with some differences in the extent of variation when species were compared. Mean isotopic signatures and average trophic diversity were relatively similar between species (Table 5), with scalloped hammerheads exhibiting a larger isotopic niche area ($TA = 9.08$, $SEAc = 2.30$, $KUD = 2.50$) and variability than Carolina hammerheads ($TA = 7.51$, $SEAc = 1.82$, $KUD = 1.68$).

Isotopic variation may be attributed to temporal effects. For example, both Carolina and scalloped hammerhead plasma $\delta^{15}\text{N}$ values differed across years ($\chi^2_3 = 22.9$, $p < 0.001$ and $\chi^2_3 = 15.0$, $p < 0.01$, respectively) but not $\delta^{13}\text{C}$ ($\chi^2_3 = 4.44$, $p = 0.22$, $\chi^2_3 = 7.40$, $p = 0.06$, respectively). Differences were attributed to uneven sampling of umbilical scar healing

stages across years; therefore, data were pooled across years to examine the effect of USS and month between species. There were intraspecific differences across USS for Carolina and scalloped hammerheads in $\delta^{15}\text{N}$ ($\chi^2_2 = 38.23$, $p < 0.001$, $\chi^2_2 = 36.85$, $p < 0.001$, respectively; Table 6), with a steady decrease in $\delta^{15}\text{N}$ for both species with the progression of umbilical scar healing (i.e. time since birth; Fig. 3A). Carolina hammerhead $\delta^{15}\text{N}$ values were consistently higher than scalloped hammerheads within each USS. By comparison, there was less change in $\delta^{13}\text{C}$ across USS, with both species exhibiting a slight increase as they aged ($\chi^2_2 = 10.14$, $p < 0.01$, $\chi^2_2 = 6.09$, $p = 0.05$; Table 5). Changes across $\delta^{15}\text{N}$ resulted in varying degrees of interspecific overlap, with the smallest overlap in USS1 and larger overlaps in USS2 and USS3 (Fig. 3A).

Comparison by month reflected a similar pattern to that of USS. There were intraspecific differences across months for Carolina and scalloped hammerheads in $\delta^{15}\text{N}$ ($\chi^2_3 = 49.39$, $p < 0.001$, $\chi^2_3 = 39.96$, $p < 0.001$, respectively; Table 6, Fig. 4A,B), with both species exhibiting an overall decrease in $\delta^{15}\text{N}$ between May and August. While Carolina hammerhead values decreased steadily across all months of sampling, scalloped hammerhead values dropped until July and remained steady in August. Therefore, when compared by month, there was a distinct difference in $\delta^{15}\text{N}$ between species, in which Carolina hammerhead $\delta^{15}\text{N}$ values were consistently higher across months (except for August) than those of the scal-

Table 5. Summary of young-of-the-year (YOY) hammerhead fork length (FL) ranges, capture date range, and isotopic metrics from sharks caught in Bulls Bay, SC, by species (Carolina, scalloped, or hybrid hammerhead), umbilical scar stage (USS1: unhealed scar; USS2: well-healed but visible scar; USS3: no visible scar), and month captured. Isotopic niche size was estimated by 3 metrics: total area of the convex hull (TA), standard ellipse area corrected for small sample sizes (SEAc), and kernel density (KUD) based on 40% core isotopic region. CD (mean distance to the centroid) represents the average degree of trophic diversity within a species. Groups with sample sizes less than 10 were removed from KUD calculations (July for both species and USS1 for Carolina hammerhead)

Tissue	Species	Group	n	FL (mm) range	Month/day of capture	$\delta^{13}\text{C}$ mean \pm SD	$\delta^{15}\text{N}$ mean \pm SD	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range	TA	SEAc	KUD	CD
Plasma	Carolina	All	61	276–500	5/6–8/30	-17.14 ± 0.33	13.57 ± 1.75	1.83	5.80	7.51	1.82	1.68	1.54
	Scalloped	All	56	316–535	5/6–8/22	-17.29 ± 0.49	13.51 ± 1.48	2.76	5.48	9.08	2.30	2.50	1.36
	Hybrid	All	17	319–493	5/11–8/27	-17.21 ± 0.28	12.99 ± 1.39	1.10	5.83	3.14	1.29	1.02	1.07
Muscle	Carolina	All	68	276–500	5/6–8/30	-16.43 ± 0.35	16.42 ± 1.07	1.95	5.19	5.97	1.19	0.98	0.97
	Scalloped	All	56	316–535	5/6–8/22	-15.80 ± 0.35	15.77 ± 1.22	1.93	4.47	6.72	1.29	1.38	1.12
	Hybrid	All	17	319–493	5/11–8/27	-16.19 ± 0.27	16.16 ± 1.06	1.16	3.51	2.28	0.92	1.04	0.99
Plasma	Carolina	USS1	9	276–325	5/6–6/8	-17.17 ± 0.38	16.35 ± 0.96	1.30	2.90	1.77	1.16	–	0.79
		USS2	16	276–394	5/6–7/13	-17.36 ± 0.36	14.48 ± 1.37	1.45	4.42	3.57	1.60	1.83	1.15
		USS3	36	339–500	5/24–8/30	-17.04 ± 0.26	12.47 ± 0.81	1.15	4.14	2.72	0.70	0.53	0.63
	Scalloped	USS1	10	316–390	5/6–6/3	-17.21 ± 0.37	15.08 ± 0.85	1.27	2.56	1.43	1.01	0.96	0.79
		USS2	28	318–468	5/11–7/19	-17.44 ± 0.55	13.95 ± 1.09	2.76	4.54	7.03	1.88	1.57	0.99
		USS3	18	405–535	6/22–8/22	-17.11 ± 0.37	11.94 ± 0.65	1.27	2.45	2.05	0.80	0.85	0.64
Muscle	Carolina	USS1	9	276–325	5/6–6/8	-16.31 ± 0.25	17.71 ± 0.72	0.77	2.50	0.56	0.34	–	0.56
		USS2	16	276–394	5/6–7/13	-16.34 ± 0.38	17.33 ± 0.75	1.48	3.15	2.51	0.92	0.50	0.67
		USS3	43	339–500	5/24–8/30	-16.48 ± 0.35	15.80 ± 0.67	1.95	3.64	3.01	0.74	0.63	0.61
	Scalloped	USS1	10	316–390	5/6–6/3	-15.58 ± 0.19	16.01 ± 1.21	0.60	3.47	1.13	0.79	0.91	1.04
		USS2	28	318–468	5/11–7/19	-15.75 ± 0.31	16.30 ± 1.13	1.38	4.47	4.00	1.05	0.75	0.88
		USS3	18	405–535	6/22–8/22	-16.00 ± 0.39	14.81 ± 0.71	1.80	2.77	2.45	0.87	0.51	0.63
Plasma	Carolina	May	11	276–339	–	-17.23 ± 0.36	16.51 ± 0.67	1.27	2.13	1.49	0.76	0.78	0.63
		June	12	276–368	–	-17.31 ± 0.31	14.58 ± 0.97	0.97	3.70	1.69	0.92	0.95	0.77
		July	8	342–394	–	-17.22 ± 0.49	13.11 ± 0.35	1.59	1.07	0.71	0.58	–	0.48
		Aug	30	360–500	–	-17.02 ± 0.25	12.22 ± 0.42	0.97	1.44	0.98	0.32	0.47	0.44
	Scalloped	May	14	316–398	–	-17.34 ± 0.43	14.94 ± 0.79	1.81	2.86	1.84	0.86	0.85	0.73
		June	25	318–440	–	-17.40 ± 0.58	13.88 ± 1.03	2.76	3.97	6.37	1.81	1.53	0.94
		July	6	405–477	–	-17.18 ± 0.29	11.81 ± 0.35	0.71	0.98	0.37	0.40	–	0.40
		Aug	11	428–535	–	-17.04 ± 0.32	11.77 ± 0.56	0.87	2.10	0.98	0.61	0.53	0.52
Muscle	Carolina	May	11	276–339	–	-16.22 ± 0.32	17.51 ± 0.99	0.92	3.77	2.03	1.10	0.98	0.80
		June	13	276–368	–	-16.37 ± 0.30	17.45 ± 0.53	1.25	1.95	1.43	0.54	0.29	0.49
		July	8	342–394	–	-16.52 ± 0.23	16.83 ± 0.50	0.74	1.39	0.55	0.41	–	0.48
		Aug	36	360–500	–	-16.49 ± 0.38	15.62 ± 0.53	1.95	2.96	2.47	0.60	0.55	0.52
	Scalloped	May	14	316–398	–	-15.59 ± 0.21	16.25 ± 0.85	0.67	2.54	1.15	0.59	0.78	0.75
		June	25	318–440	–	-15.74 ± 0.39	16.19 ± 1.32	1.93	4.47	6.56	1.68	0.91	1.07
		July	6	405–477	–	-16.10 ± 0.17	15.14 ± 0.49	0.41	1.20	0.34	0.31	–	0.43
		Aug	11	428–535	–	-16.06 ± 0.22	14.53 ± 0.39	0.73	1.25	0.49	0.30	0.34	0.39

loped hammerheads. By contrast, $\delta^{13}\text{C}$ values were relatively similar across months, although Carolina hammerhead values differed significantly while scalloped hammerhead values did not ($\chi^2_3 = 9.35$, $p = 0.03$, $\chi^2_3 = 6.38$, $p = 0.10$). There was a slight but steady increase in $\delta^{13}\text{C}$ between May and August for both species (Fig. 4C,D). The temporal changes in $\delta^{15}\text{N}$ resulted in little overlap among plasma ellipses of any month for Carolina hammerheads, while there was some degree of overlap across scalloped hammerheads between May and June as well as the July and August ellipses (Fig. S4A).

Latitudinally, only a comparison of scalloped hammerheads caught in Florida and South Carolina could

be made due to limited and uneven plasma samples from Georgia. Florida scalloped hammerhead $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were higher (14.02 ± 1.35 and -16.69 ± 0.65 , respectively) than those of South Carolina (13.41 ± 1.54 and -17.28 ± 0.53 ; Fig. S5A), although South Carolina had a larger variability in $\delta^{13}\text{C}$ than Florida.

3.3.2. Muscle

Carolina hammerhead muscle $\delta^{13}\text{C}$ was significantly lower than scalloped hammerheads ($W = 388$, $p < 0.001$), while $\delta^{15}\text{N}$ was significantly higher ($W = 2439$,

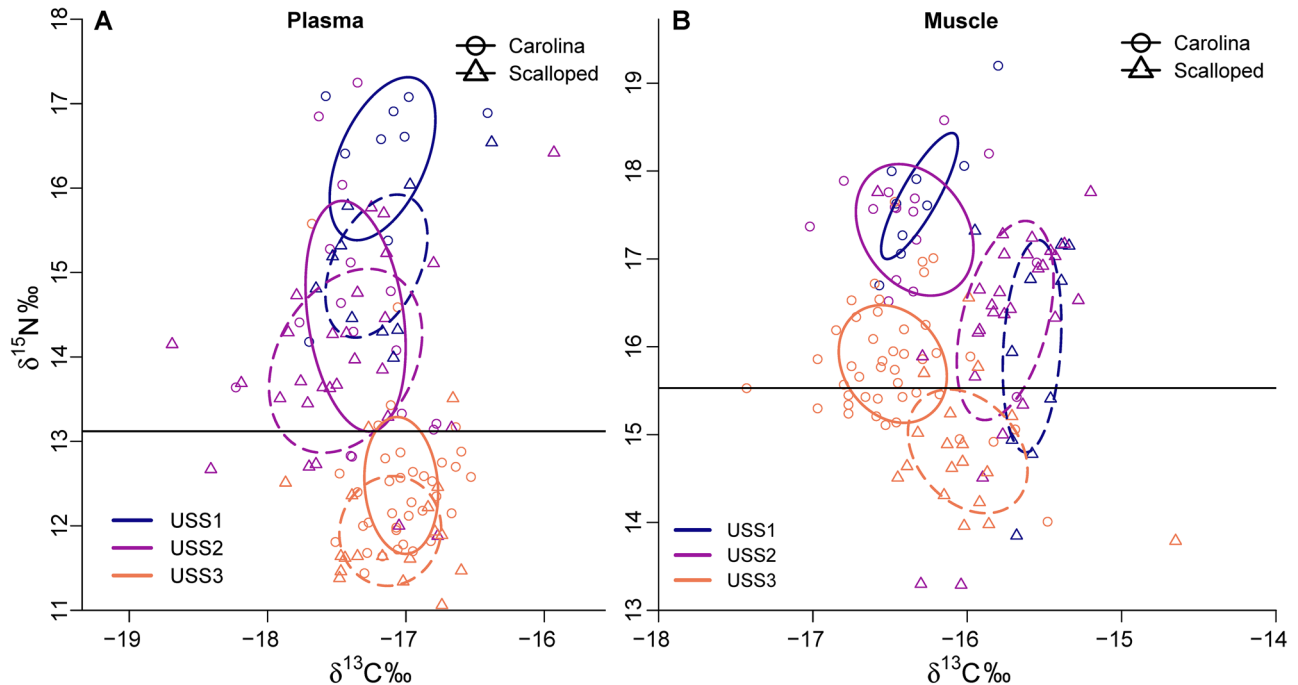


Fig. 3. Standard ellipses of isotopic signatures by umbilical scar stage (USS) in Carolina and scalloped hammerheads within (A) muscle and (B) plasma samples from Bulls Bay. USS1: unhealed or partially healed; USS2: well-healed; USS3: fully healed, no scar present. The horizontal black lines are a reference for the $\delta^{15}\text{N}$ muscle mean ($n = 8$, 15.53 ± 0.59 SD) and $\delta^{15}\text{N}$ plasma mean ($n = 8$, 13.12 ± 1.14 SD) values for mature male scalloped hammerheads that were collected offshore in SC on their respective plots

Table 6. Non-parametric (Kruskal-Wallis) stable isotope results from comparison between month, umbilical scar stage (USS), and year by species (Carolina hammerhead *Sphyrna gilberti* or scalloped hammerhead *S. lewini*) and tissue (plasma and muscle), and hammerhead (HH) group (Carolina, scalloped or hybrid) by tissue in Bulls Bay, South Carolina

Isotope	Species	Variable	Plasma				Muscle			
			n	χ^2	df	p	n	χ^2	df	p
$\delta^{13}\text{C}$	Carolina	USS	61	10.14	2	<0.01	68	3.84	2	0.15
		Month	61	9.35	3	0.03	68	6.10	3	0.11
		Year	61	4.44	3	0.22	68	7.78	3	0.05
	Scalloped	USS	56	6.09	2	0.05	56	17.17	2	<0.001
		Month	56	6.38	3	0.10	56	21.124	3	<0.001
		Year	56	7.40	3	0.06	56	13.47	3	<0.01
	All	HH group	134	4.86	2	0.09	141	64.35	2	<0.001
$\delta^{15}\text{N}$	Carolina	USS	61	38.23	2	<0.001	68	36.85	2	<0.001
		Month	61	49.39	3	<0.001	68	45.21	3	<0.001
		Year	61	22.91	3	<0.001	68	17.94	3	<0.001
	Scalloped	USS	56	35.86	2	<0.001	56	17.52	2	<0.001
		Month	56	39.96	3	<0.001	56	19.59	3	<0.001
		Year	56	14.96	3	<0.01	56	0.42	3	0.94
	All	HH group	134	1.32	2	0.52	141	7.53	2	0.02

$p < 0.01$). This pattern was reiterated when comparing hammerheads at USS1 ($W = 1$, $p < 0.001$ and $W = 81$, $p < 0.01$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively; Table 5). Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were similar to plasma for hammerheads sampled in Bulls Bay (small in the former, large in the latter; Fig. S3B). Likewise, scal-

loped hammerheads occupied a larger isotopic niche area and had higher variability in resource use than Carolina hammerheads ($TA = 6.72$ and 5.97 , $SEAC = 1.29$ and 1.19 , and $KUD = 1.38$ and 0.98 , respectively; Table 5). There was no niche overlap between species regardless of method.

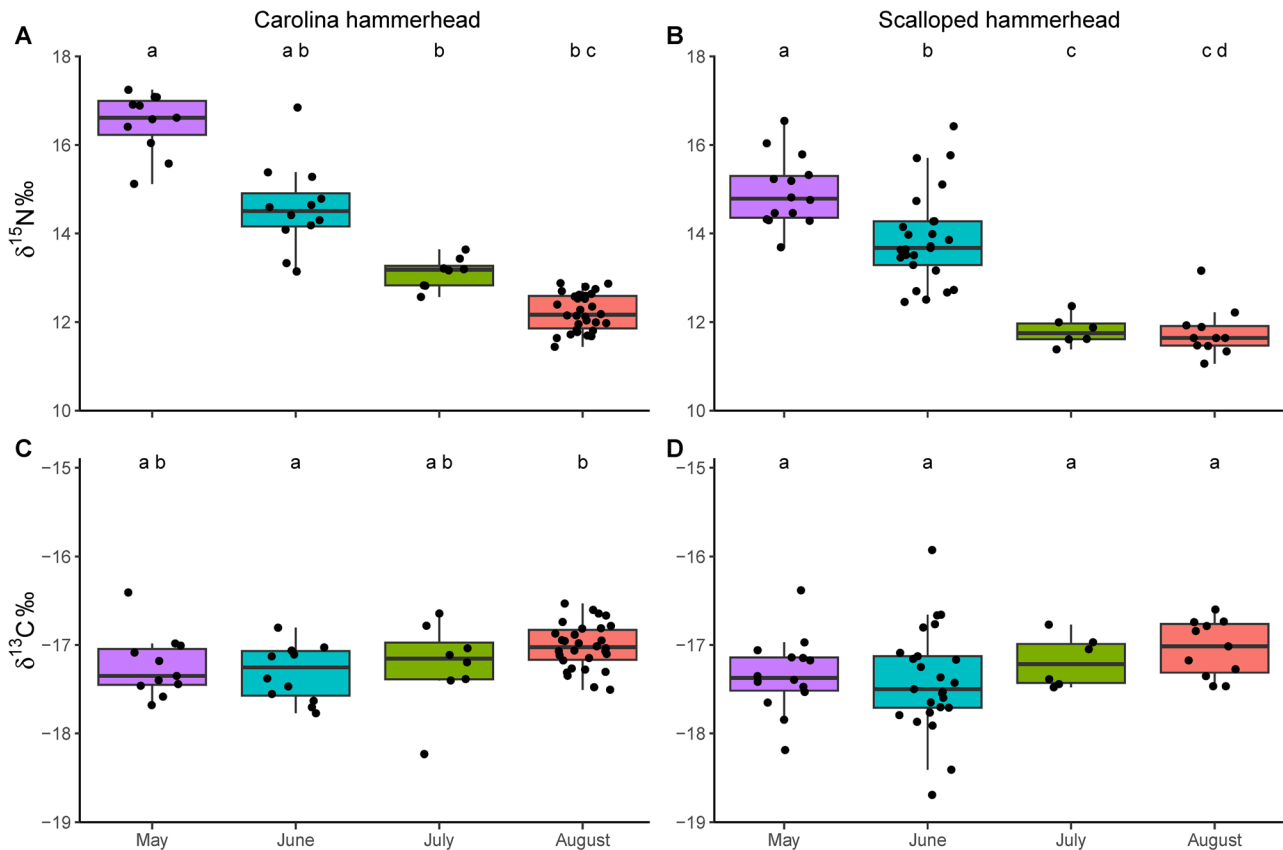


Fig. 4. Boxplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences in plasma across month of capture for (A,C) Carolina and (B,D) scalloped hammerheads in Bulls Bay, SC. The top and bottom of the box correspond to the 25th and 75th percentiles, the horizontal bar in the box is the median, the whiskers represent $1.5 \times \text{IQR}$ and dots reflect individual hammerhead values. Months denoted by a different lowercase letter indicate significant differences between $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Tukey's HSD test, $p < 0.05$)

The effect of USS on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ varied for both species. There was no difference in $\delta^{13}\text{C}$ across USS for Carolina hammerheads ($\chi^2 = 3.84$, $p = 0.15$). By contrast, $\delta^{13}\text{C}$ decreased for scalloped hammerheads with time since birth ($\chi^2_2 = 17.17$, $p < 0.001$; Table 6). Within each USS, $\delta^{13}\text{C}$ was distinctly lower in Carolina hammerheads. Generally, both species exhibited a decrease in $\delta^{15}\text{N}$ with time since birth ($\chi^2_2 = 36.85$, $p < 0.001$, $\chi^2_2 = 17.52$, $p < 0.001$, respectively; Table 6). Carolina hammerheads exhibited a steady decrease in $\delta^{15}\text{N}$ with time since birth, while $\delta^{15}\text{N}$ values remained similar between USS1 and USS2 before decreasing for scalloped hammerheads (Fig. 3B). Similar to plasma, Carolina hammerhead muscle $\delta^{15}\text{N}$ values were consistently higher within each USS. Large interspecific differences in $\delta^{13}\text{C}$ resulted in no overlap for the youngest hammerheads (USS1 and USS2), but a slight overlap between species with USS3 (Fig. 3B). Within each species, there was moderate overlap between USS1 and USS2 but little to no overlap between those stages and USS3 (Fig. 3B).

The temporal pattern found in plasma was similarly reflected in muscle for Carolina hammerheads, in which $\delta^{15}\text{N}$ values differed across sampling years ($\chi^2_3 = 17.94$, $p < 0.001$) but $\delta^{13}\text{C}$ values did not ($\chi^2_3 = 7.78$, $p = 0.05$; Table 6). By contrast, scalloped hammerhead muscle $\delta^{15}\text{N}$ values did not differ across years, and there was a difference among years in $\delta^{13}\text{C}$ ($\chi^2_3 = 13.47$, $p < 0.01$; Table 6). Annual differences are likely an artefact of uneven sampling across months, and as such, samples were pooled across years by species.

Both Carolina and scalloped hammerhead stable isotopes differed across months. For Carolina hammerheads, only $\delta^{15}\text{N}$ changed ($\chi^2_3 = 45.21$, $p < 0.001$; Table 6), with August samples being significantly lower ($p < 0.001$) than May, June, and July, which were not different from each other ($p > 0.10$; Fig. 5A). For scalloped hammerheads, both muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed across months ($\chi^2_3 = 21.12$, $p < 0.001$, $\chi^2_3 = 19.59$, $p < 0.001$, respectively). $\delta^{15}\text{N}$ values were higher in May and June than in August (Fig. 5B), while

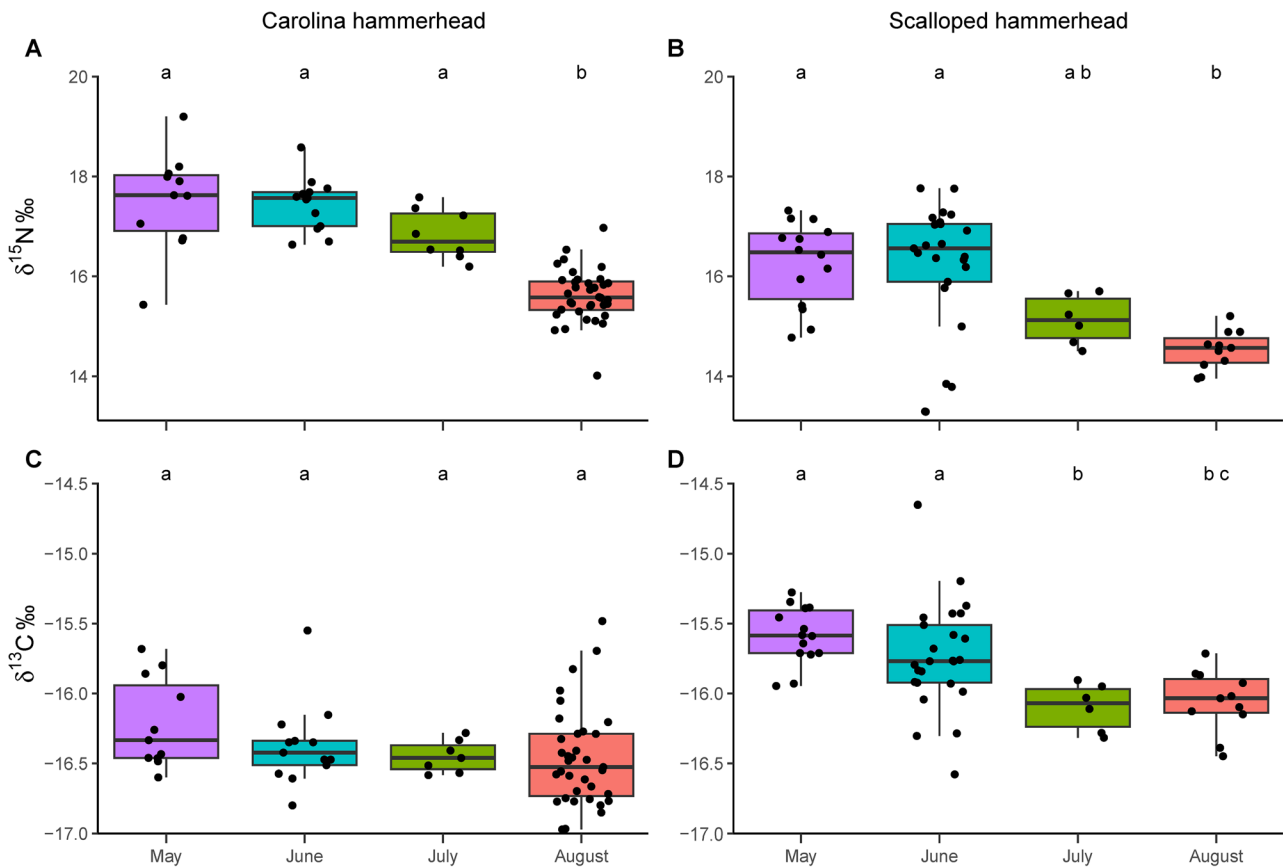


Fig. 5. Boxplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences in muscle across month of capture for (A,C) Carolina and (B,D) scalloped hammerheads in Bulls Bay, SC. Months denoted by a different letter lowercase indicate significant differences between $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Tukey's HSD test, $p < 0.05$). See Fig. 4 for boxplot description

$\delta^{13}\text{C}$ values were higher in May and June than in July and August (Fig. 5D). Both species had similar SEAc trends in muscle among months, with high intraspecific niche overlap between May and June, but little to no overlap between July and August (Fig. S4B). Mean muscle $\delta^{13}\text{C}$ values remained distinct between species over time, in which Carolina hammerhead $\delta^{13}\text{C}$ was more negative. Though the mean values became less distinct in July and August, no interspecific overlap occurred between the ellipses within each month.

When muscle isotopic values were compared across states, Carolina hammerheads were consistently lower in $\delta^{13}\text{C}$ and higher in $\delta^{15}\text{N}$ than those of scalloped hammerheads (Fig. S5B), reiterating interspecific results from Bulls Bay (Table 5, Figs. 3B & 5). Carolina hammerhead isotope values varied across states, in which hammerheads from Georgia and South Carolina had similar $\delta^{13}\text{C}$ values that were higher than Florida, but hammerheads from South Carolina and Florida had similar $\delta^{15}\text{N}$ values but lower than those from Georgia (Table S4, Fig. S5B). Scalloped hammerheads were

similar across states in both isotopes, especially in $\delta^{13}\text{C}$ (Table S4, Fig. S5B). Scalloped hammerheads between states had a high isotopic overlap, while there was less overlap between states in Carolina hammerheads due to the variation in both isotopes (Fig. S5B).

3.3.3. Sulfur

Variation was high for $\delta^{34}\text{S}$ muscle values, ranging from 12.81 to 19.21‰, which were both from individuals caught in late summer (August and September) and early fall. The $\delta^{34}\text{S}$ values from hammerheads caught in spring (April and May) ranged from 15.69 to 18.72‰. $\delta^{34}\text{S}$ decreased with increased fork length for both species (Fig. 6A). Likewise, Carolina and scalloped hammerheads caught in South Carolina early in the season had significantly higher $\delta^{34}\text{S}$ values compared to those sampled later in the summer within species ($t_{15} = 4.24$, $p < 0.001$ and Welch's $t_9 = 2.55$, $p = 0.03$, respectively; Fig. 6B). However, when the species

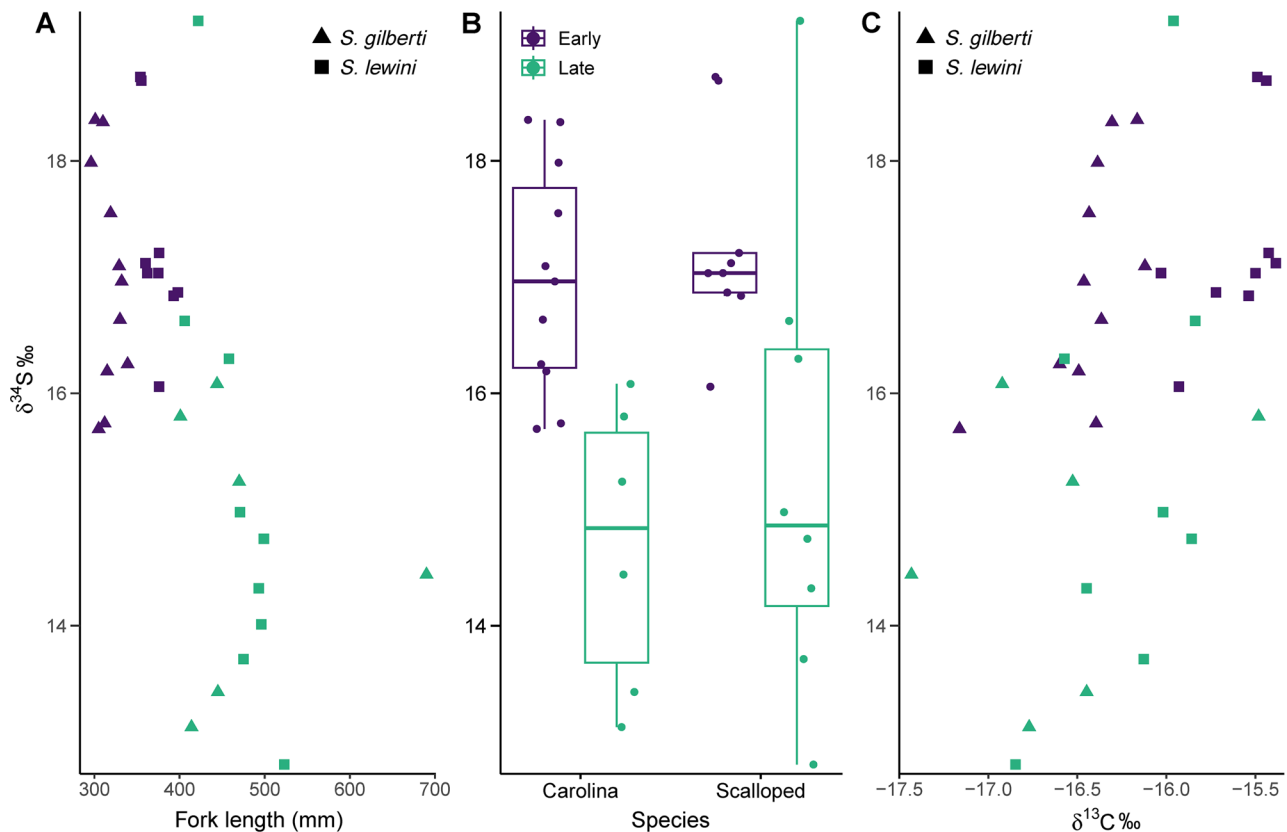


Fig. 6. Comparison of (A) $\delta^{34}\text{S}$ vs. fork length (mm), (B) interspecific comparison of $\delta^{34}\text{S}$ values between Carolina *Sphyrna gilberti* and scalloped *S. lewini* hammerheads captured in South Carolina in spring (early) and late summer (late), and (C) $\delta^{13}\text{C}$ vs. $\delta^{34}\text{S}$. The early period (in purple across panels) includes sharks caught in April and May, which reflect the mother's diet and habitat, while the late period (in green across panels) includes sharks caught in August, September, and early fall, which reflect the young-of-the-year diet in the nursery. (B) See Fig. 4 for boxplot description

were compared within early or late summer, $\delta^{34}\text{S}$ values were similar ($p = 0.46$ and $p = 0.66$, respectively). When comparing $\delta^{34}\text{S}$ to $\delta^{13}\text{C}$ (Fig. 6C), Carolina hammerheads caught early had similarly high $\delta^{34}\text{S}$ values ($16.98 \pm 0.98\text{‰}$) to scalloped hammerheads ($17.29 \pm 0.87\text{‰}$) but had more negative $\delta^{13}\text{C}$ values.

3.4. Hybrids

Hybrid diet composition (as assessed by prey categories) was similar to the diets of both Carolina and scalloped hammerheads (Table S1). Identified prey were mostly sciaenids (39.86% IRI_M) and shrimp (40.62% IRI_M). Star drum were the most important identifiable prey item (23.93% IRI_M), closely followed by penaeid shrimp (21.40 IRI_M). The digestion status of hybrid prey items spanned from fresh to completely digested, with an almost equal proportion of prey items with DC2, DC3, and DC4 (30.2, 27.4, and 35.9%, respectively). Two out of 34 hybrid stomachs

were empty (5.9%), and both these samples were from hammerheads with unhealed umbilical scars (USS1).

Hybrid muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values fell within the range of both Carolina and scalloped hammerheads, in which hybrid $\delta^{13}\text{C}$ was higher than Carolina and lower than scalloped hammerheads, while hybrid $\delta^{15}\text{N}$ was lower than Carolina but higher than scalloped hammerheads (Table 5, Fig. S3B). Nevertheless, hybrid muscle isotope values were more similar to Carolina hammerheads than scalloped hammerheads (Fig. S3B). When the 3 groups were compared, $\delta^{13}\text{C}$ values in Carolina hammerheads and hybrids were more similar (Dunn's $p = 0.03$) than in scalloped hammerheads and hybrids (Dunn's $p < 0.01$). Hybrid $\delta^{15}\text{N}$ values were not different from either species (Dunn's $p > 0.98$). As such, there was greater isotopic niche overlap in muscle between Carolina hammerheads and hybrids than between scalloped hammerheads and hybrids (Table 4). There were no differences between hybrids and either species in plasma isotope values (Kruskal-Wallis, $p >$

0.08 for both isotopes). Hybrid metrics (TA and SEAc) were lower than either species for both tissues, which is likely a reflection of a smaller sample size.

4. DISCUSSION

This study provides the first species-specific trophic ecology data on cryptic Carolina hammerheads and scalloped hammerheads from the western North Atlantic Ocean. The results are not consistent with resource partitioning in the youngest hammerheads, as YOY scalloped and Carolina hammerheads had similar generalist diets in shared nursery grounds. However, maternally influenced isotopic signatures (muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between the species indicated that gestating females feed at different trophic levels and/or occupy different habitats.

4.1. YOY diet

Broadly, YOY hammerheads throughout their global distribution appear to rely on prey from similar (or functionally similar) taxa and thus display similar feeding habits. In the southeastern USA, diets consisted mostly of sciaenids (which included at least 10 species), engraulids, penaeid shrimp, and squid. A relatively similar diet for YOY and juvenile scalloped hammerheads was described in northwestern Florida by Bethea et al. (2011), primarily comprising small teleosts (mainly bothids and sciaenids) and penaeid shrimp. Though some of the sciaenids found in the Gulf were similar to those found in this study, the importance of sciaenids overall, especially star drum, was vastly different between studies and more important to the diet of hammerheads in this study (IRI_M 26.68% vs. 1.47% in the Gulf). When assessing diet by prey category, the importance of teleosts, shrimp, and cephalopods was similar between diet studies, although more non-shrimp crustaceans were found in the Gulf (IRI_M 7.3% in the Gulf vs. 1.53 in Bulls Bay; Bethea et al. 2011). Other juvenile scalloped hammerhead diet studies similarly described a mostly benthic diet with some pelagic prey comprising a mix of teleosts, crustaceans (mostly shrimp), and cephalopods to varying degrees of importance (Bornatowski et al. 2014, Torres-Rojas et al. 2015, Rosende-Pereiro et al. 2020, Galindo et al. 2021).

Hammerheads in the southeastern USA appear to have ample access to food resources based on the low proportion of empty stomachs. When empty stomachs were found, they tended to be in the earliest USS

(those with open or partially healed umbilical scars), estimated to be less than 2 wk old (Duncan & Holland 2006). Other studies have also observed empty stomachs in neonates (Bush 2003, Rosende-Pereiro et al. 2020) and attributed it to a possible non-feeding period, inefficient hunting skills, or lack of prey abundance. While the majority of empty stomachs observed in the present study occurred in the youngest hammerheads, the rate of empty stomachs (3.7% all YOY, 16.2% for hammerheads with open to partially healed umbilical scars) was quite low in comparison to studies in other localities (i.e. 20 and 15% empty for all YOY and 59 and 41% in neonates from Hawaii and the Pacific coast of Mexico, respectively; Bush 2003, Rosende-Pereiro et al. 2020). The results of this study suggest that hammerheads are able to feed at a young age, and the availability of local prey resources may be driving contrasting results among the studies.

The high degree of fullness and wide breadth of prey items across all stomachs suggests that hammerheads feed indiscriminately, regardless of age. Across months, prey categories varied by importance. The lack of consistency and associated high variability in the importance of diet categories across all YOY age classes, in conjunction with stomach fullness, indicates that opportunism is an effective strategy for sharks that exhibit a generalist feeding behavior in habitats with ample sources of prey. Indiscriminate feeding may be a necessity for young hammerheads as they seem to rapidly deplete maternally provided energy stores in the liver (Lyons et al. 2020). Without sufficient prey resources, hammerheads would likely starve to death soon after birth or exhibit reduced growth and condition, increasing the likelihood of predation (Duncan & Holland 2006). As such, food resource availability in nursery habitats likely plays an important role in hammerhead early life survivorship.

Though overall prey categories were similar in hammerhead diet along the southeastern USA, prey species and dietary proportions differed latitudinally. Hammerheads sampled from Bulls Bay, South Carolina, had at least 27 prey items identified to species compared to 17 for Georgia and Florida combined. This difference may be an artefact of the lower numbers of hammerheads sampled from Georgia and Florida, but it could also reflect differences in habitat quality, including prey availability. Bulls Bay is located within the Cape Romain National Wildlife Refuge and, due to conservation efforts and limited surrounding development, is relatively pristine, supporting a wide variety of small fishes, crustaceans, and squid (Shaw et al. 2016). Sampling in Bulls Bay mainly occurred along open coastline adjacent to an

extensive network of tidal creeks and marsh habitat. By contrast, hammerheads sampled in Georgia and Florida were mostly collected from nearshore habitats that included open ocean and sand flats associated with beaches (Cape Canaveral), some with shallow shoals adjacent to deeper troughs, and marsh habitat along an intracoastal waterway (Tolomato River). Though the Tolomato River is located within the Guana Tolomato Matanzas National Estuarine Research Reserve, increased boating traffic and dock construction within the Reserve can impact benthic resources and habitat (https://coast.noaa.gov/data/docs/nerrs/Reserves_GTM_SiteProfile.pdf), which could result in a loss of suitable habitat for juveniles of important fish species and other potential prey items for young hammerheads. In addition, YOY hammerheads were collected off Cape Canaveral in late spring and early summer when phytoplankton biomass tends to be lower due to influence of oligotrophic Gulf Stream waters (Stelling et al. 2023). Primary productivity, water quality, and habitat quality can affect both prey abundances and assemblages and this might partially explain lower prey richness in hammerheads caught in Florida. In a study on nursery grounds for lemon sharks *Negaprion brevirostris* near Cape Canaveral, some juveniles were in relatively poor condition, possibly due to limited prey resources or quality (Reyier et al. 2008). Lyons et al. (2020) found potentially lower growth rates in YOY hammerheads from Florida compared to more northern locations (Georgia and South Carolina), which could similarly suggest a limited prey availability or availability of lower-quality prey species in this southern region.

Niche partitioning between YOY Carolina and scalloped hammerheads was not detected and could be attributed to the high prey productivity of Bulls Bay. The Pianka observed dietary overlap values were consistently higher than those of the simulated values, suggesting that there may be a lack of competition or that competition has not yet led to resource partitioning (Bethea et al. 2007). Resources in Bulls Bay are likely abundant enough to support multiple, functionally similar species in the same area while limiting competition (Shaw et al. 2016). Competition between hammerhead species may also be reduced through species-specific life history characteristics, which can lead to temporal resource partitioning. In Bulls Bay, scalloped hammerhead abundance peaks earlier in the summer (mid-July) compared to Carolina hammerheads, which are most abundant a month later in August, resulting from purportedly offset parturition windows between the species (Barker et al. 2021). Differences in arrival time to the nursery could

lead to reduced competition if demand for shared resources is temporally offset (Paine 1963, Sandercock 1967, Ross 1986). Furthermore, scalloped hammerheads are born at larger sizes (Quattro et al. 2013, Lyons et al. 2020), so although the prey items may overlap, the 2 species may be feeding on prey of different sizes, which would reduce direct competition (Dayan & Simberloff 2005, Bethea et al. 2011, Hussey et al. 2011). Intraspecific variation in diet can also be a potential method of partitioning. Though stomachs from both species often contained multiple prey taxa per stomach, Carolina hammerhead stomachs were less diverse and their $\delta^{13}\text{C}$ range was narrower than that of scalloped hammerheads, signifying that Carolina hammerheads may target the same prey items more often (i.e. exhibit more specialist habits), which could reduce competition.

4.2. Maternal ecology inferences

Though caution is needed to interpret stable isotopes of YOY hammerheads due to maternal influence on values, this phenomenon was leveraged to gain insights into species-specific maternal feeding ecology. In particular, muscle was assumed to be attributable to maternal feeding rather than YOY exogenous feeding due to its longer turnover and the fact that comparisons were made in the first few months of life. As such, the significant difference in $\delta^{13}\text{C}$ between the 2 hammerhead species suggests that maternal ecology differs. Inherent isotopic variability is low in scalloped hammerhead litters (0.09 and 0.08‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively; Vaudo et al. 2010). The magnitude of difference seen in isotope values between hammerhead species is much larger than those of the inherent variability, signifying a true difference in resource use between gestating females. In addition, isotopic variability of litters *in utero* is likely different from YOY and even neonate sharks since they all receive similar provisioning but will have varying environmental and dietary influences on their isotopic values after birth.

Gradients of $\delta^{13}\text{C}$ values in the marine environment are related to the isotopic signatures of food web bases, and benthically linked inshore habitats are more enriched in ^{13}C relative to offshore phytoplankton-based food webs (France 1995, Hobson 1999). Therefore, more negative values observed in YOY Carolina hammerheads may suggest that adult females feed in more offshore environments than adult female scalloped hammerheads. Alternatively, differences in $\delta^{13}\text{C}$ could indicate that adult females forage

in the same areas but feed primarily on prey resources from different food webs, which have different carbon baselines (e.g. benthic elasmobranchs vs. pelagic squid).

Sulfur isotopes suggest mature female Carolina and scalloped hammerheads share prey resources, or at least both consume a high proportion of prey from the same food web. Due to limited trophic fractionation, $\delta^{34}\text{S}$ is a conservative tracer and can be used to distinguish production source, and higher $\delta^{34}\text{S}$ values are associated with plankton (i.e. pelagic food webs) as compared to more benthic, coastal values (Peterson et al. 1986, Connolly et al. 2004, Chasar et al. 2005). The high values of the youngest YOY Carolina and scalloped hammerheads suggest mature females of both species share pelagic-based feeding habits. However, when paired with $\delta^{13}\text{C}$, the more depleted $\delta^{13}\text{C}$ values in YOY Carolina hammerheads suggest adult females inhabit waters further offshore compared to scalloped hammerhead females. No genetically confirmed adult female Carolina hammerheads and limited adult female scalloped hammerheads have been sampled despite various survey efforts conducted along the US southeast coast. These hypotheses provide insights into potential habitats of these 2 species; that said, directed research (i.e. capture and tagging) will be necessary to confirm purported habitat differences.

In terms of trophic positioning (i.e. $\delta^{15}\text{N}$), adult females were inferred to feed at fairly high levels. To place values into context, mature male and older juvenile scalloped hammerheads were opportunistically sampled in waters nearshore and offshore of South Carolina in late April and early May. Scalloped hammerheads with unhealed umbilical scars had higher $\delta^{15}\text{N}$ values than the sampled older juveniles and mature males. Scalloped hammerhead embryo $\delta^{15}\text{N}$ values can be higher relative to their mother (Vaudo et al. 2010), which has been found for other elasmobranchs (McMeans et al. 2009, Olin et al. 2011). Considering enrichment of the youngest YOY individuals, it is likely that mature female scalloped hammerheads have a trophic position comparable to the mature males in this study and to other scalloped hammerheads across their distribution (Hussey et al. 2015, Loor-Andrade et al. 2015, Estupiñán-Montaño et al. 2017). Carolina hammerheads had a higher $\delta^{15}\text{N}$ than scalloped hammerheads, suggesting the mature Carolina hammerhead females may feed at a higher trophic level or on prey with a more enriched ^{15}N baseline.

Hybrids provided a unique opportunity to corroborate the influence of hammerhead maternal ecology on the isotopic signatures of YOY because these indi-

viduals have parentage from both lineages but should only reflect the isotopic signals of their mothers, assuming they inherit those signals through nutritive resources provided during gestation. Consistent with this idea, hybrids were found to more closely resemble Carolina hammerhead YOYs in isotopic signatures of slow turnover tissues, which mirrored genetic information that nearly all hybrids had Carolina hammerhead mothers (Barker et al. 2019). In fast turnover tissues, hybrids appeared similar to Carolina and scalloped hammerheads, indicating no difference in their feeding ecology, at least in Bulls Bay.

4.3. Maternal signal loss

As predicted, the loss of maternal isotopic signal was most prominent in plasma, which has a relatively short half-life (~22 and 33 d for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively; Kim et al. 2012, Malpica-Cruz et al. 2012), as hammerheads grow and create tissues that reflect their own diet and/or habitat within the nursery. Both tissues showed a decrease in $\delta^{15}\text{N}$ between hammerheads with unhealed umbilical scars and those with no scar (USS3), but the magnitude of loss is larger in plasma (~3.5‰) than in muscle (~1.6‰). This implies that isotopic values across USS reflect maternal signal loss in both tissues, although the muscle lags behind the plasma due to its longer incorporation rate (months to years in elasmobranchs; MacNeil et al. 2006, Logan & Lutcavage 2010, Kim et al. 2012). In particular, the significant decrease in plasma $\delta^{15}\text{N}$ is likely attributed to YOY hammerheads feeding at lower trophic positions than their mothers. The diet of mature Carolina or scalloped hammerheads has not been described in the North Atlantic Ocean; however, in other ocean basins, adult female hammerheads are known to mainly feed on a variety of fishes, including other elasmobranchs, and pelagic cephalopods (Klimley 1983, Bornatowski et al. 2014). It is probable that mature individuals in the western North Atlantic have a similar diet, while stomach content analysis of YOYs was dominated by fishes from lower trophic levels and invertebrates. A similar loss of maternal signal in YOY hammerheads was described in the Mexican Pacific, where $\delta^{15}\text{N}$ significantly decreased with length (Rosende-Pereiro et al. 2020) and has been noted in other YOY elasmobranchs (Matich et al. 2010, 2015, Olin et al. 2011, Belicka et al. 2012).

Carolina and scalloped hammerhead mean muscle $\delta^{15}\text{N}$ values differed by 1.9 and 1.2‰, respectively, between USS1 and USS3, exceeding the reported scalloped hammerhead mother–embryo discrimination factor of 0.82‰ in Vaudo et al. (2010). Intraspecific dif-

ferences in muscle $\delta^{13}\text{C}$ values between USS1 and USS3 individuals were much less than the reported value of 1.01‰ (Vaudo et al. 2010), at 0.17 and 0.42‰ for Carolina and scalloped hammerheads, respectively. The minimal change across $\delta^{13}\text{C}$ suggests that USS3 sharks are approaching maternal signal replacement in their muscle but with limited assimilation of their new diet reflected in their isotopic values, while a large $\delta^{15}\text{N}$ difference suggests nearly full assimilation of diet and completion of maternal signal replacement (Olin et al. 2011). The change in $\delta^{13}\text{C}$, or lack thereof, between USS1 and USS3 sharks may be confounded by the dynamics of estuarine waters, where there are multiple primary producers (Connolly et al. 2004, Seubert et al. 2019). Including $\delta^{34}\text{S}$ as an additional tracer can provide more resolution of an animal's diet than $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values alone (Connolly et al. 2004, Seubert et al. 2019). Both Carolina and scalloped hammerheads caught in late April and early May (i.e. neonates) were much more enriched in ^{34}S (by 2.29 and 1.96‰, respectively) than those caught in late summer, indicating that there was a change in resource use between the youngest (i.e. those reflective of their mothers) and oldest YOY in this study. $\delta^{34}\text{S}$ has the potential to identify foraging habitats and foraging strategies along a benthic-to-pelagic gradient, particularly in estuaries (Peterson & Fry 1987, Connolly et al. 2004).

It is difficult to determine exactly when YOY hammerheads begin losing their maternal signal due to protracted birth windows, variation in length-at-birth, and inability to age animals to within weeks or months after umbilical scars are healed. Some studies suggest that maternal signals could remain in muscle for 1 yr or more (MacNeil et al. 2006, Logan & Lutcavage 2010, Matich et al. 2010, Niella et al. 2021); however, by August (within 4 mo, conservatively assuming animals were born in May) there were some YOY hammerhead $\delta^{15}\text{N}$ values that fell below the reference male adults, suggesting that their muscle may show some incorporation of their estuarine diet and that tissue turnover may be more rapid in YOY hammerheads than in other shark species. Fast metabolic turnover in neonate to YOY leopard sharks *Triakis semifasciata* contributed to the expedited loss of maternal signals (Malpica-Cruz et al. 2012), although rate of loss is likely species-specific. Young hammerheads are known to have high metabolic rates (Lowe 2002) and rapidly transition from maternally derived to exogenously obtained resources (Lyons et al. 2020, present study); therefore, it would not be surprising if stable isotope tissue turnover rates were higher in YOY hammerheads than in other elasmobranch species.

5. CONCLUSIONS

YOY hammerhead sharks share a similar generalist diet across the southeastern USA with no clear difference in dietary niche. Despite YOY scalloped hammerheads being ~50 mm (on average) longer than Carolina hammerheads (Barker et al. 2021, Lyons et al. 2020), the 2 species have a large dietary overlap regardless of metric (i.e. stomach contents or plasma stable isotopes). However, stable isotope values for YOY muscle, a tissue that integrates information over a longer time scale, indicate that adult female hammerheads may use different prey resources or different habitats. These differences are erased as hammerheads grow and incorporate local signatures into their tissues. Bulls Bay and other nurseries along the southeast US coast are productive areas that provide young hammerheads with the necessary resources to survive their first months of life, which highlights the importance of establishing and maintaining essential fish habitat (EFH) along the coast. Both hammerhead species exhibit a diverse diet and regularly had full stomachs, stressing the importance of these areas across the southeast Atlantic coast as nursery grounds for young hammerheads.

Many limitations exist for studying mature Carolina and scalloped hammerheads off the southeastern USA, including their indistinguishable external morphology, costliness of sampling, and relative scarcity. Considering these constraints, muscle isotope values from neonatal hammerheads provide valuable insight into adult feeding ecology, presenting evidence that females of these species likely feed in different habitats and/or at different trophic levels. By extension, adult movements may also differ, which could present conservation challenges for species that are managed as a single homogenous group. Furthermore, nearly unidirectional hybridization (i.e. female Carolina hammerheads mate with male scalloped hammerheads and F1 hybrids almost always backcross into scalloped hammerheads; Barker et al. 2019) could eventually lead to the loss of the Carolina hammerhead. Taken together, the seemingly more limited distribution of Carolina hammerheads compared to scalloped hammerheads and the threat of hybridization could make this species more susceptible to overfishing and more sensitive to degradation of EFH.

Preservation of intact, functional nurseries may play an outsized role in the conservation of the Carolina hammerhead, which appears to rely on these resources heavily during its early life history. A single EFH boundary for nursery areas, particularly for Bulls Bay, is suitable for both hammerhead species consid-

ering the large resource overlap between neonates. The largest data gaps in the southeastern USA for either species pertain to adult biology, and management recommendations would benefit greatly from filling these gaps by opportunistically collecting (i.e. through fishery-independent surveys or commercial fisheries) more tissue samples from mature hammerheads for genetic identification and/or SIA to further investigate adult resource use.

It is imperative to establish baseline data such as life history, reproductive physiology, habitat use, and trophic ecology for all stages of the Carolina hammerhead, and to update existing data for the sympatric scalloped hammerhead population in order to monitor changes in the species over time. Knowledge of the trophic ecology of these sympatric and cryptic hammerheads across their life stages and habitats will allow for appropriate conservation and management decisions and add to the breadth of information required for potential ecosystem-based fishery management.

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