Estuaries and Coasts
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Comparative Dietary Diversity and Trophic Ecology of Two Estuarine Mesopredators

Andrea M. Kroetz[1,2] · **J. Marcus Drymon**[1,2] · **Sean P. Powers**[1,2]

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Abstract Quantifying the trophic dynamics of mesopredators in coastal habitats is an essential precursor to understanding their role in linking multiple trophic levels. Traditional dietary analyses may miss key aspects of a species' feeding ecology and may thus fail to identify trophic linkages between predators and economically important prey populations. We applied stomach content and stable isotope analyses to estimate diet and trophic dynamics and investigated intraspecific dietary diversity of bonnetheads (*Sphyrna tiburo*) and red drum (*Sciaenops ocellatus*). Both juvenile and adult bonnetheads and juvenile red drum had diets comprised mainly of crustaceans, notably portunid crabs and penaeid shrimp, with varying degrees of dietary and isotopic niche overlap. Juvenile and adult bonnetheads had high dietary and isotopic niche overlap, whereas the degree of overlap between bonnetheads and red drum varied. Our findings indicate that bonnetheads are dietary specialists whereas red drum are dietary generalists. Further analysis identified intraspecific variability in the diet of each species; adult bonnetheads had the highest prey diversity whereas red drum had the lowest. We show that dietary and isotopic niche overlap and intraspecific variation in diet exist among juvenile and adult bonnetheads and juvenile red drum, though to varying degrees. Our findings demonstrate the importance of fully examining the trophic ecology of species that share habitats and resources, both at individual and population levels.

Keywords Stable isotopes · Stomach contents · Trophic ecology · Dietary diversity · Coastal ecosystems · Estuarine fishes

Introduction

Food web structure is a compilation of the presence, abundance, and trophic interactions of all species within ecological communities. Mesopredators, here defined as trophically mid-ranking predators in a food web (Prugh et al. 2009), are often overlooked but provide vital links between upper trophic levels and primary consumers (Ritchie and Johnson 2009). Declines in large elasmobranchs (Ferretti et al. 2010; Worm et al. 2013; Dulvy et al. 2014) and other large predatory fish (Ward and Myers 2005; Kitchell et al. 2006) are well acknowledged and emphasize the importance of mesopredators through predation release and trophic cascades, particularly in coastal ecosystems. Understanding trophic structure and predator-prey interactions in coastal food webs is critical for predicting the effects of predator declines and shifts in food availability attributed to human and natural causes (Garvey et al. 1998; Vander Zanden et al. 2000; Wetherbee and Cortés 2004; Vaudo and Heithaus 2011).

Stomach content analysis is traditionally used to describe the diet of a species (Hyslop 1980) as it is a direct assessment of what a predator has consumed. High taxonomic resolution can be achieved with this analysis and prey items can often be quantified; however, this type of analysis has limitations. For example, stomach contents only provide insight into what the predator has eaten over relatively short time scales. In addition, opportunistically consumed prey may appear to be an

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✉ Andrea M. Kroetz
akroetz2@gmail.com

1 Department of Marine Sciences, University of South Alabama, LSCB 25, Mobile, AL 36688, USA

2 Dauphin Island Sea Lab, 101 Bienville Blvd, Dauphin Island, AL 36528, USA

important dietary component, without being representative of the long-term diet. These issues could lead to errors in predicting trophic levels (Polunin and Pinnegar 2002), and hence faulty inferences of the importance of predation on economically important prey. Stable isotope analysis provides a complementary method that reduces biases associated with stomach content analysis. Carbon and nitrogen stable isotope values from consumed prey are assimilated and integrated into the tissues of the consumer providing long-term dietary information (Fry 2006). Stable isotope analysis provides increased analytical capacity to understand food web structure and trophic interactions of populations. Using both techniques provides a robust description of a species' diet and its trophic relationships.

Stomach content and stable isotope analyses provide the opportunity to describe intraspecific patterns and variation in trophic interactions. Individual conspecific predators may use a variety of diet resources that are available, thus creating variation in trophic interactions (Bolnick et al. 2003). Quantifying dietary variability can provide insight into intra- and interspecific competition and potential resource partitioning that may occur. Recent studies suggest considerable intraspecific variability in trophic interactions across many taxa including large-bodied coastal predators (Matich et al. 2011; Kernaléguen et al. 2015; Rosenblatt et al. 2015). Understanding individual differences in diet is becoming an increasingly important component to understanding trophic niche widths of predators (Rosenblatt et al. 2015). While intraspecific variation has been increasingly characterized in large marine predators (Matich et al. 2011; Matich and Heithaus 2015; Rosenblatt et al. 2015), little information is available for mesopredators.

Bonnetheads (*Sphyrna tiburo*) and red drum (*Sciaenops ocellatus*) are important mesopredators in coastal ecosystems. Both species spend extensive portions of their lives in estuaries (Murphy and Taylor 1990; Compagno 1984). For example, larval and juvenile red drum depend on estuaries as nursery habitat until maturity is reached at 3–6 years of age (Murphy and Taylor 1990; Rooker and Holt 1997). Similarly, bonnetheads spend considerable amounts of time within estuaries (Heupel et al. 2006; Ubeda et al. 2009) and often return to specific estuaries over the course of several years (Driggers et al. 2014; Kroetz et al. 2015). Previous work has shown considerable overlap in habitat use and trophic interactions of these species, with red drum exhibiting more generalized diets (Overstreet and Heard 1978; Scharf and Schlight 2000; Facendola and Scharf 2012) than bonnetheads (Cortés et al. 1996). Both species have been suggested to undergo ontogenetic shifts in diet in the Gulf of Mexico (GOM; Llansó et al. 1998; Scharf and Schlight 2000; Bethea et al. 2007; Facendola and Scharf 2012) and have been documented to consume crabs and shrimp with teleosts comprising a larger portion of red drum diet compared with bonnetheads (Overstreet and Heard 1978; Cortés et al. 1996; Scharf and Schlight 2000; Bethea et al. 2007; Facendola and Scharf 2012). Despite these ecological similarities, the degree to which individuals within these populations demonstrate trophic overlap remains unknown.

Given the documented spatial estuarine overlap, we initiated a comprehensive investigation to examine the trophic dynamics of bonnetheads and red drum in the northern GOM. We used complementary stomach content and stable isotope analyses, combined with metrics of dietary and isotopic niche overlap and intraspecific dietary variability to achieve a robust description of the trophic dynamics between these co-occurring mesopredators. The goals of this study were to (1) describe the diet and identify the major dietary components of each species and life stage, (2) assess the degree of dietary and isotopic niche overlap between the two species, and (3) determine the extent of intraspecific variation in the diet of each species.

Methods

Sample Collection

Juvenile and adult bonnetheads were collected primarily from fishery-independent gillnet surveys conducted in the northern GOM, as well as opportunistically from commercial gillnet fishermen in Alabama state waters (Fig. 1). Bonnetheads collected for stomach samples were measured (stretch total length in cm), weighed (kg), and sex and life stage were determined. Bonnetheads were classified as either juvenile or adult based on maturity. Life stage for males was determined externally by the development of the claspers following Clark and von Schmidt (1965) and maturity in females was determined from length-maturity relationships in the GOM (Southeast Data, Assessment, and Review 2013). Red drum collected for stomach samples were obtained through the Alabama Department of Conservation and Natural Resources Marine Resources Division (ADCNR MRD) monthly fishery-independent gillnet surveys and opportunistically from a fishery-dependent survey through the Alabama Deep Sea Fishing Rodeo (ADSFR) (Fig. 1). Red drum were measured (stretch total length in cm), weighed (kg), and sexed. Red drum were also classified as either juvenile or adult based on maturity, and this was assessed based on length-at-age relationships for red drum in the northern GOM (Hightower 2013). All stomach samples for both species were collected from 2009 to 2014. Stomachs collected in the field were immediately placed on ice and subsequently frozen in a −20 °C freezer. Potential prey items of bonnetheads and red drum were collected by ADCNR MRD Fisheries Assessment and Monitoring Program (FAMP) trawl surveys conducted in Mississippi Sound and Mobile Bay, AL during the course of this study (Fig. 1). A 5-m otter trawl with 40 × 60-cm wooden doors, 35-

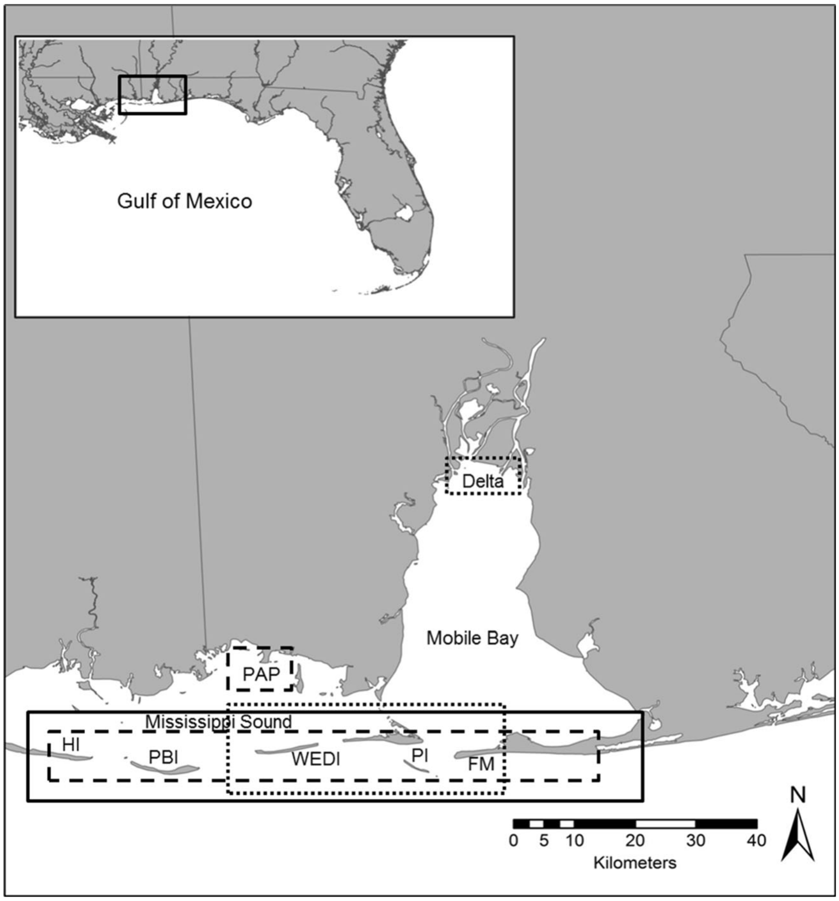

Fig. 1 General sampling and collection locations of bonnetheads and red drum for stomach content and stable isotope samples. Bonnethead sampling locations are represented by *large dashed lines*, red drum by the *small dotted line*, and potential prey items by the *solid line*. *HI* Horn Island, *PBI* Petit Bois Island, *PAP* Point Aux Pins, *WEDI* West end of Dauphin Island, *PI* Pelican Island, *FM* Fort Morgan. Collection locations of sampled fish indicate spatial overlap between the species

mm stretch mesh with a 45-mm cod-end fitted with a 4.7-mm liner was used to collect prey base samples.

Stomach Content Analysis and Dietary Overlap

Stomachs were thawed and contents were rinsed over a 500-μm sieve. Prey items were extracted and identified to the lowest taxonomic level possible and identifiable prey items were weighed (g wet weight). Identifiable contents were categorized into general taxonomic groups as follows: (1) crabs, (2) shrimp, (3) crustaceans other than crabs and shrimps, (4) teleosts, (5) vegetation (plant/wood material), (6) cephalopods, and (7) other molluscs. Cumulative prey curves (Ferry and Cailliet 1996) were generated using PRIMER v6 by plotting the cumulative number of prey taxa based on the lowest possible level of identification across all samples. Bias of sampling chronology on the curve was removed via randomization across 999 permutations and the curves were quantitatively assessed (Bizzarro et al. 2007) to determine if a sufficient sample size was collected.

The contributions of stomach content items to diets were reported using percentage by number (%*N*), percentage by weight (%*W*), and percentage frequency of occurrence (%*O*) (Hyslop 1980) and were used to calculate percent index of relative importance (%IRI; Cortés 1999). In order to examine relative prey importance and diet overlap among juvenile and adult bonnetheads and juvenile red drum, %*N* and %*W* were calculated per individual stomach and then averaged for each prey type to provide mean proportions (%MN and %MW, respectively) and variances for prey items (Chipps and Garvey 2007). The dietary importance of prey items on an individual basis was examined through a diagram that relates prey abundance to frequency of occurrence (Costello 1990; Amundsen et al. 1996). The graph indicates a generalized or specialized feeding strategy, relative prey importance (dominant or rare), and niche variation (individual vs. population patterns) based on individual prey types that would otherwise not be determined from single diet measures (Costello 1990; Amundsen et al. 1996; Chipps and Garvey 2007). Prey-specific abundance was calculated for each life stage of bonnetheads and red drum by dividing the total abundance of a specific prey item by the total abundance of all prey items found in the stomachs that contain that prey item (i.e., excludes stomachs that do not contain the prey item). A generalist feeding strategy is typified by high prey diversity and low abundance of each prey type whereas a specialist strategy is typified by low prey diversity and high use of a few prey types (Bridcut and Giller 1995). Overall differences in stomach content data among the three groups were assessed by a one-way multivariate analysis of similarity (ANOSIM) on a Bray-Curtis adjusted similarity index run in PRIMER v6.

Pianka's niche overlap (Pianka 1976) was calculated using *%W* and *%N* and was compared with a null model (RA3 algorithm, 1000 repetitions) to assess overlap. This null model approach was calculated in R statistical platform 3.1.1 using the package EcoSimR (Gotelli et al. 2015). Values of Pianka's niche overlap index close to 0 reflect usage of exclusive resource categories by the species being compared whereas values close to 1 reflect similar resource use at the alpha = 0.05 significance level (Gotelli et al. 2015).

Stable Isotope and Niche Overlap Analysis

Muscle tissue from a subset of individuals examined for stomach content analysis was collected for stable isotope analysis. For this subset of individuals and for teleosts that were potential prey items, a section of white muscle below the primary dorsal fin (Estrada et al. 2003; MacNeil et al. 2005) was extracted. For all other potential prey items, white muscle tissue was extracted from the organisms where available (i.e., claws in crabs, mid-section of shrimp). In the laboratory, muscle tissue was rinsed with deionized water and placed in a Labconco freeze-dry system and dried for a period of 24 h. Once completely dry, the muscle tissue was ground into a fine powder with a mortar and pestle and packed in tin capsules (Elementar Americas) in 2 mg (±0.05) aliquots for stable isotope analysis. Samples were sent to the University of California Davis Stable Isotope Facility where a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20/20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) was used to determine $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios. During analysis, samples were interspersed with several replicates of at least two different laboratory standards (previously calibrated against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, USGS-40, and USGS-41) with Pee Dee Belemnite as the standard reference material for C and atmospheric N_2 for N. The experimental precision (standard deviation of replicates of the standard) for $\delta^{13}C$ was 0.2 and 0.3 ‰ for $\delta^{15}N$. The C/N ratio of all predator and potential prey item samples analyzed was <3.5; thus, lipids were not extracted from tissues (Post et al. 2007).

Differences in mean $\delta^{13}C$ and $\delta^{15}N$ of juvenile and adult bonnetheads and juvenile red drum were analyzed using multivariate analysis of variance (MANOVA). Data for juvenile and adult bonnetheads were pooled if no significant differences were found in mean $\delta^{13}C$ and $\delta^{15}N$ across sampled regions (Fig. 1) and year sampled. If significant differences were found, Bonferroni corrections were applied and pairwise comparisons were used to determine which group or groups were different. Assumptions of normality were assessed post hoc by examining the residuals from the MANOVA. To determine if $\delta^{13}C$ and $\delta^{15}N$ signatures changed as a function of body size (i.e., a proxy for ontogenetic shifts in diet), we used linear regression models. If no significant changes in $\delta^{13}C$ and $\delta^{15}N$ were present, then it was inferred that long-term diet did not change as the fish reached larger sizes. The relative contributions of prey items to the isotopic signature of bonnetheads and red drum were estimated using the isotope mixing model Stable Isotope Analysis in R (SIAR; Parnell and Jackson 2013). Three prey categories making up the majority of dietary contributions as identified by stomach contents were used in the model to obtain defined results.

Quantitative metrics (known as Layman metrics) to assess trophic structure were calculated following Layman et al. (2007). Metrics included mean distance to centroid (CD), mean nearest-neighbor distance (M-NND), and standard deviation of nearest-neighbor distance (SD-NND). The CD provided the average degree of trophic diversity within a food web, and the M-NND and SD-NND represented density and evenness of species packing in isotopic niche space, respectively (Layman et al. 2007). To determine isotopic niche width of each group sampled, a combination of metrics was applied. Standard ellipse area (SEA) and total area (TA), as represented by convex hulls, were used to estimate the isotopic niches of sampled groups. Convex hull area (TA) encompasses all samples from each species in the $\delta^{13}C$–$\delta^{15}N$ bi-plot space and represents the total amount of occupied niche space by a group (i.e., juvenile bonnetheads, adult bonnetheads, juvenile red drum); this then serves as a proxy for total extent of trophic diversity within a food web (Layman et al. 2007). Standard ellipse areas corrected for sample size (SEA_C) represent the bivariate standard deviation of the data and are insensitive to bias associated with small sample size (Jackson et al. 2011). The SEA_C can be used to identify potential interspecific competition for prey by evaluating the extent of overlap of the ellipse areas (Jackson et al. 2011). The TA and SEA_C were calculated using Stable Isotope Bayesian Ellipses in R (SIBER) via the package SIAR (Jackson et al. 2011; Parnell and Jackson 2013).

Intraspecific Variation

Intraspecific variation in the diets of juvenile and adult bonnetheads and juvenile red drum was assessed on stomach content data using the Shannon-Weaver diversity index (H′) (Shannon and Weaver 1963). We analyzed each stomach separately to obtain a quantitative measure of prey diversity that was consumed by each animal. The higher the value of H′, the more diverse the diet is of that particular animal. We applied non-parametric Kruskal-Wallis test on the H′ values to determine if there were significant differences in prey diversity among juvenile and adult bonnetheads and juvenile red drum. Pairwise multiple comparisons among groups were assessed using Dunn's post hoc analysis. Analyses were run in R using the packages stats and PMCMR.

Table 1 Biological data for bonnetheads and red drum sampled in the northern Gulf of Mexico for stomach content analysis

Category	Number	FL (cm ± SE)	TL (cm ± SE)	Weight (kg ± SE)
All bonnetheads	120	71.0 (1.1)	88.5 (1.4)	3.2 (0.2)
Males	48	69.4 (1.7)	86.3 (2.1)	2.8 (0.2)
Females	72	71.9 (1.5)	89.9 (1.8)	3.4 (0.2)
Adults	83	77.4 (0.9)	96.3 (1.0)	3.9 (0.2)
Juveniles	37	56.6 (1.3)	71.0 (1.6)	1.6 (0.1)
Juvenile red drum	151	53.1 (0.6)	55.7 (0.6)	1.8 (0.1)
Males	43	52.1 (1.2)	54.6 (1.2)	1.8 (0.1)
Females	96	53.7 (0.7)	56.4 (0.7)	1.9 (0.1)
Undifferentiated	12	51.9 (2.0)	54.2 (2.0)	1.7 (0.2)

Sizes are reported in fork length (FL) and total length (TL) with standard error (SE) for all fish

Results

Bonnetheads

A total of 120 stomachs were collected from juvenile and adult bonnetheads. Both females ($n = 72$) and males ($n = 48$) were sampled across juvenile (mean FL = 56.6 ± 1.3 cm SE, $n = 37$) and adult (mean FL = 77.4 ± 0.9 cm SE, $n = 83$) life stages (Table 1). Of the 120 stomachs, 116 stomachs (96.7 %) contained prey items and four stomachs (3.3 %) were empty. For juveniles, 35 stomachs (94.6 %) contained prey items and two stomachs (5.4 %) were empty. For the adults, 81 stomachs (97.6 %) contained prey items while two stomachs (2.4 %) were empty. Quantitative analysis of cumulative prey curves (Bizzarro et al. 2007) for juveniles (Fig. 2a) indicated that a sufficient sample size was achieved to describe the diet for juveniles ($p > 0.05$, Fig. 2a) whereas additional stomachs would have improved the accuracy of the diet description for adults ($p < 0.04$, Fig. 2b). Dietary metrics indicated that crabs were the most abundant prey category for both juvenile and adult bonnetheads, followed by shrimp (Table 2). For crabs, four families and five species were identified while four families and one species of shrimp were identified (Table 3). Teleosts were the third most dominant prey item for juvenile bonnetheads while cephalopods, other molluscs, and other crustaceans comprised <1 % (%MN and %MW) each (Table 2). Teleosts, cephalopods, other molluscs, and other crustaceans comprised <1 % (%MN and %MW) each of adult bonnethead diet (Table 2).

Muscle samples extracted from juvenile and adult bonnetheads ($n = 58$) were analyzed for $\delta^{13}C$ and $\delta^{15}N$ values. Isotope data for each life stage were pooled across regions and year since no significant differences in $\delta^{13}C$ and $\delta^{15}N$ were found (MANOVA, $F_{5,\ 52} = 1.24$, $p > 0.30$ for region; MANOVA, $F_{3,\ 54} = 2.02$, $p > 0.07$ for year). Mean values of both $\delta^{13}C$ and $\delta^{15}N$ were very similar for both life stages (Table 4). Linear regressions did not detect changes in $\delta^{13}C$ and $\delta^{15}N$ values as a function of size ($F = 1.05$, $p > 0.31$) possibly indicating that diet did not change with ontogeny. Source contributions from the top three prey groups that made up >98 % of the %IRI from SIAR analysis indicated that crabs contributed the most to juvenile (median value, 60 %) and adult (70 %) bonnethead diet (Fig. 3a, b, respectively). Shrimp were the second highest contributors to the diets of juvenile (20 %) and adult (25 %) bonnetheads.

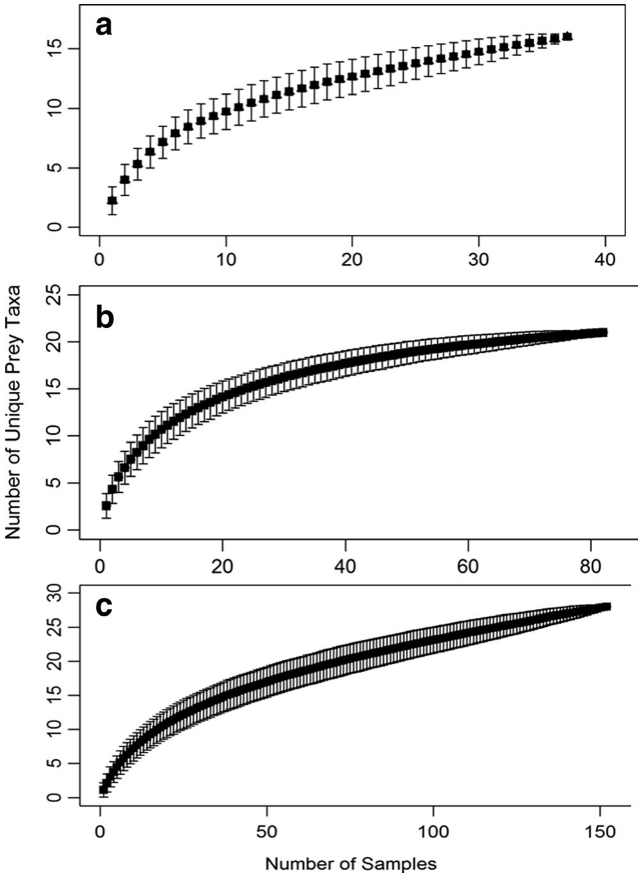

Fig. 2 Cumulative prey curves from **a** juvenile bonnetheads, **b** adult bonnetheads, and **c** juvenile red drum. Note that the scales are different to accommodate the different number of unique prey taxa and number of stomachs sampled. *Error bars* represent standard deviations around a resampled mean after 999 iterations

Table 2 Dietary metrics representing mean percent by number (%MN), mean percent by weight (%MW), percent occurrence (%*O*), percent index of relative importance (%IRI), and relative prey importance (P_i) as a function of broad prey category for juvenile and adult bonnetheads and juvenile red drum

Prey taxon	%MN (±SE)	%MW (±SE)	%*O*	%IRI	%P_i
Crabs					
Adult bonnethead	71.9 (3.7)	76.9 (4.1)	95.10	87.90	85.90
Juvenile bonnethead	58.7 (7.0)	64.1 (7.1)	85.70	83.80	78.00
Juvenile red drum	33.3 (4.2)	31.3 (4.2)	43.80	33.40	58.50
Shrimp					
Adult bonnethead	23.8 (3.5)	15.1 (3.2)	44.40	10.60	30.20
Juvenile bonnethead	26.9 (6.3)	21.0 (5.9)	40.00	14.70	47.60
Juvenile red drum	39.6 (4.3)	41.7 (4.4)	51.40	49.40	68.10
Teleosts					
Adult bonnethead	0.48 (0.3)	0.04 (0.0)	2.50	0.01	39.50
Juvenile bonnethead	6.10 (3.2)	7.40 (3.9)	14.30	1.50	54.20
Juvenile red drum	25.8 (3.8)	25.7 (3.9)	37.10	22.50	72.70
Cephalopods					
Adult bonnethead	0.30 (0.3)	0.05 (0.1)	1.20	0.00	40.80
Juvenile bonnethead	0.00 (0.0)	0.00 (0.0)	0.00	0.00	0.00
Juvenile red drum	0.24 (0.2)	0.01 (0.0)	0.95	0.00	1.60
Other Molluscs					
Adult bonnethead	0.70 (0.5)	0.02 (0.0)	2.50	0.01	0.79
Juvenile bonnethead	0.69 (0.7)	0.09 (0.1)	2.90	0.02	3.20
Juvenile red drum	0.07 (0.1)	0.02 (0.0)	0.95	0.00	2.20
Other crustaceans					
Adult bonnethead	0.41 (0.3)	0.04 (0.0)	2.50	0.00	2.00
Juvenile bonnethead	0.00 (0.0)	0.00 (0.0)	0.00	0.00	0.00
Juvenile red drum	0.00 (0.0)	0.00 (0.0)	0.00	0.00	0.00
Plant material					
Adult bonnethead	–	0.64 (0.3)	13.60	–	2.80
Juvenile bonnethead	–	3.98 (2.8)	31.40	–	1.90
Juvenile red drum	–	1.18 (0.8)	14.30	–	4.30

Red Drum

Red drum stomach contents were analyzed from 151 individuals. Mean fork length of red drum sampled was 53.1 cm (±0.6 mm SE) and both male (n = 43), female (n = 96), and undetermined (i.e., sex could not be determined due to undeveloped ovaries or testes; n = 12) red drum were sampled (Table 1). Based on recent length-at-age data for this species in the northern GOM, the red drum collected for this study fall within the size range of fish age 0–3 years and were thus classified as juveniles (Hightower 2013). Of the 151 stomachs analyzed, 105 (69.5 %) contained prey items and 46 (30.5 %) stomachs were empty. Analysis of the cumulative prey curve for red drum (Fig. 2c) indicated that a sufficient sample size was reached ($p > 0.05$) to describe the diet. Shrimp were the most abundant prey category closely followed by crabs (Table 2). For shrimp, three families were identified whereas four families and one species of crab were identified (Table 3). Teleosts were the third most important prey category (Table 2) with six families and five species able to be identified (Table 3). Cephalopods, other molluscs, and other crustaceans comprised <1 % (%MN and %MW) each of the diet of juvenile red drum.

Table 3 Reported stomach contents of juvenile and adult bonnetheads and juvenile red drum collected in this study

Prey Category	Juvenile bonnethead	Adult bonnethead	Juvenile red drum
Crabs			
Family			
Albuneidae			X
Diogenidae		X	
Menippidae			X
Pinnotheridae		X	
Polybiidae	X	X	
Portunidae	X	X	X
Xanthidae			X
Species			
Arenaeus cribrarius	X	X	
Callinectes sapidus	X	X	X
Callinectes similis		X	
Clibanarius vittatus		X	
Ovalipes floridanus	X	X	
Shrimp			
Family			
Alpheidae	X	X	
Callianassidae	X	X	X
Palaemonidae			X
Penaeidae	X	X	X
Squillidae	X	X	
Species			
Squilla empusa	X	X	
Cephalopods			
Family			
Loliginidae		X	X
Fishes			
Family			
Batrachoididae			X
Blenniidae			X
Clupeidae			X
Engraulidae			X
Sciaenidae			X
Trichiuridae			X
Species			
Anchoa mitchilli			X
Brevoortia patronus			X
Cynoscion arenarius			X
Micropogonias undulatus			X
Opsanus tau			X
Unidentifiable fish	X	X	X
Plant			
Plant matter (seagrass, twigs)	X	X	X

Prey items were identified to the lowest taxonomic level possible and "X" denotes when a prey item was present in the stomach

Muscle samples (n = 78) extracted from individuals retained for stomach content analysis were analyzed for δ^{13}C and δ^{15}N values for comparison with bonnetheads.

Table 4 Results from statistical analyses of dietary overlap, Layman metrics, and isotope values

Species	Mean δ^{15}N (‰)	Mean δ^{13}C (‰)	TA	CD	M-NND	SD-NND	SEA	SEA$_C$	Pianka overlap				SEA$_C$ overlap
									%N	*p* value	*%W*	*p* value	
JBH	13.5 (±0.5)	−17.7 (±0.5)	1.84	0.82	0.25	0.41	0.75	0.82					
ABH	13.7 (±0.8)	−17.6 (±0.9)	11.0	0.87	0.30	0.46	1.83	1.87					
RDM	14.2 (±1.7)	−20.3 (±2.0)	58.9	2.18	0.46	0.54	10.71	10.85					
JBH vs ABH									0.94	0.06	0.90	0.02	0.75
JBH vs RDM									0.61	0.23	0.87	0.02	0.00
ABH vs RDM									0.45	0.30	0.56	0.30	0.11

Percent number (*%N*) and weight (*%W*) were used in the dietary niche overlap whereas δ^{13}C and δ^{15}N values were used in standard ellipse area (SEA) and SEA corrected for sample size (SEA$_C$) comparisons. Layman metrics are mean distance to the centroid (CD), mean nearest-neighbor distance (M-NND), and standard deviation of nearest-neighbor distance (SD-NND). Total isotopic niche space occupied (TA) and mean values for δ^{13}C and δ^{15}N of juvenile (JBH) and adult bonnetheads (ABH) and juvenile red drum (RDM) are included

Significant differences in geographic sampling were found (MANOVA, $F_{5,\ 72} = 3.40$, $p < 0.01$; Wilks $\lambda = 0.63$, $p < 0.01$) for δ^{13}C and δ^{15}N. Pairwise comparisons identified one of the six locations (Mississippi Sound) differed in δ^{13}C ($p < 0.01$) and thus this location was removed from the pooled data. The mean δ^{13}C and δ^{15}N values were slightly more enriched and depleted, respectively, compared with bonnetheads (Table 4). Linear regressions did not detect changes in δ^{13}C and δ^{15}N values as a function of total length ($F = 0.30$, $p > 0.59$) possibly indicating that red drum diet did not change with ontogeny. Source contributions from the top three prey groups that made up >98 % of the %IRI from SIAR analysis indicated that shrimp were the most important contributors to the diet (median value, 55 %) followed by teleosts (45 %) (Fig. 3c).

Dietary Overlap

Pianka's overlap index indicated that dietary niche overlap was present between juvenile and adult bonnetheads with varying degrees of overlap between bonnetheads and red drum (Table 4). With respect to *%W*, overlap of juvenile and adult bonnetheads was significant (0.90; $p = 0.02$); similarly, high overlap (0.94; $p = 0.06$) was shown with respect to *%N*. Juvenile bonnetheads and juvenile red drum had significant overlap (0.87; $p = 0.02$) with respect to *%W* and less overlap (0.61; $p = 0.23$) when calculated with *%N*. Adult bonnetheads and juvenile red drum had non-significant dietary overlap with respect to *%W* (0.56; $p = 0.30$) and *%N* (0.45; $p = 0.30$). In the feeding strategy diagram for bonnetheads, crabs were in the upper right quadrant indicating that this was a dominant prey category and had a high contribution to dietary niche width for both juveniles and adults (Fig. 4a, b). Shrimp were located in the upper right quadrant for red drum (Fig. 4c) indicating that they were a dominant prey category and also contributed the most to the dietary niche of this species, closely followed by crabs. The prey categories represented in the lower left quadrant were rare occurrences in the diet and contributed very little to the dietary niche in terms of prey-specific weight. For the bonnetheads and red drum, this included molluscs, cephalopods, other crustaceans, and plant material (Fig. 4). Teleosts were considered rare for adult bonnetheads (Fig. 4b) whereas they contributed slightly more to the diet of juvenile bonnetheads but still relatively rare (Fig. 4a). Teleosts were indicated as the third most dominant and important prey category that contributed to the diet of juvenile red drum. Multivariate analysis of the stomach content data revealed significant differences among the three groups (global $R = 0.22$, $p < 0.001$). Pairwise comparisons indicated significant differences between both juvenile bonnetheads and juvenile red drum ($R = 0.20$, $p < 0.01$) and between adult bonnetheads and juvenile red drum ($R = 0.30$, $p < 0.01$). Significant differences were found between juvenile and adult bonnetheads ($R = 0.14$, $p < 0.01$) but to a lesser degree indicating that the stomach contents of these two groups are more similar to one another. Values of δ^{15}N from bonnetheads with fish in their stomachs were compared with δ^{15}N values from bonnetheads without fish in their stomachs to determine if teleosts could have been assimilated into tissues over a longer time period. No significant differences (all bonnetheads ANOVA, $F_{1,\ 54} = 0.56$, $p > 0.46$) were found indicating that though not all bonnethead stomachs contained teleosts at the time of analysis, for those individuals without teleosts in their stomachs at the time of sampling, teleosts may have still been incorporated into the dietary isotopic signature over time. Following Bridcut and Giller (1995), results indicated that juvenile and adult bonnetheads followed more of a specialist diet strategy with some supplementation or opportunistic feeding on teleosts while red drum followed a generalist strategy.

Isotopic Niche Overlap

In general, juvenile red drum had the largest range in δ^{15}N and δ^{13}C values and were the most enriched in ^{15}N (Fig. 5). Bonnetheads were more enriched in ^{13}C compared with red drum. There was a significant difference in δ^{13}C and δ^{15}N values

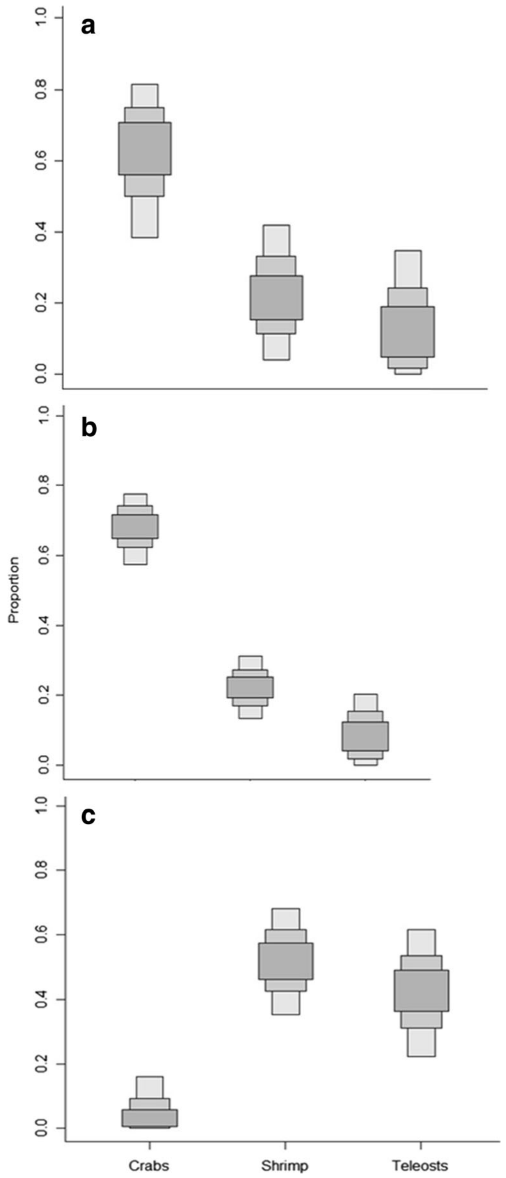

Fig. 3 Boxplots of the proportion of prey source contribution to the diet of **a** juvenile bonnetheads, **b** adult bonnetheads, and **c** juvenile red drum using a stable isotope mixing model (SIAR). The proportions show the credibility intervals at 95, 75, and 25 %

of bonnetheads and red drum (MANOVA, $F_{2,\ 133}$ = 17.5, $p < 0.01$; Wilks $\lambda = 0.58$, $p < 0.01$). Bonferroni corrections were applied and significant differences were identified in δ^{13}C values between juvenile red drum and bonnetheads ($p < 0.01$ compared with both juvenile and adult bonnetheads).

Layman metrics indicated that juvenile and adult bonnetheads were very similar isotopically (Table 4). Bonnetheads had less average isotopic variation compared with red drum indicating that they have a more specialized diet. Juvenile red drum had higher isotopic variation indicating a more generalized diet (Table 4). Juvenile red drum occupied the largest isotopic niche area (TA = 58.9 % of all niche area) followed by adult bonnetheads (TA = 11.0 %) and juvenile bonnetheads (TA = 1.84 %) (Table 4). Results from SEA_C indicated that isotope niche overlap was present (Table 4). Juvenile and adult bonnethead isotopic niche areas were highly overlapped sharing 75 % of isotopic niche area while juvenile bonnetheads and juvenile red drum shared no (0 %) isotopic niche area. Adult bonnetheads and juvenile red drum had minimum overlap sharing 11 % of isotopic niche area (Fig. 5).

Intraspecific Variation

Individuals of juvenile and adult bonnetheads and juvenile red drum showed varying degrees of dietary diversity. Individual juvenile bonnetheads had a range of H′ from 0 to 1.04 whereas individual adult bonnetheads had a slightly higher range from 0 to 1.36. Individual juvenile red drum had the largest range of H′ from 0 to 1.39. Mean individual diversity indicated that adult bonnetheads consumed the most diverse prey items (mean H′ = 0.38 ± 0.04 SE), followed by juvenile bonnetheads (mean H′ = 0.33 ± 0.06 SE), with red drum having the least diverse stomach contents among individuals (mean H′ = 0.15 ± 0.03 SE). Kruskal-Wallis analysis indicated significant differences in prey diversity ($\chi^2 = 24.4$, $df = 2$, $p < 0.01$). Post hoc pairwise comparisons indicated no significant differences between juvenile and adult bonnetheads ($p > 0.01$) whereas both life stages of bonnetheads were significantly different from juvenile red drum ($p < 0.01$ for both comparisons), indicating that red drum are driving the observed differences.

Discussion

Overlap in resource use can lead to competition among mesopredator species, which can alter trophic pathways and demand for shared resources (Woodland et al. 2011). Drivers such as differences in life history, physiology, ontogenetic niche shifts, and differences in behavior among individuals within populations can reduce overlap and enable coexistence. This may be important for food web structure and ecosystem resilience to perturbations, which is a growing concern in coastal ecosystems (Folke et al. 2004; Oliver et al. 2015).

The application of stomach content and stable isotope analyses together provided comprehensive information on the trophic ecology of potentially competing mesopredators as well as provided insight into intraspecific variation in diet. Our data suggest that bonnetheads have a relatively narrow dietary and isotopic niche width compared with a wider niche in red drum. Interestingly, both bonnetheads and red drum relied heavily on crustaceans in their diets, though they fed on different families and species of crustaceans. Portunid crabs, callianassid, and penaeid shrimps were the only groups of prey that were consumed by both species while the rest of the diets were

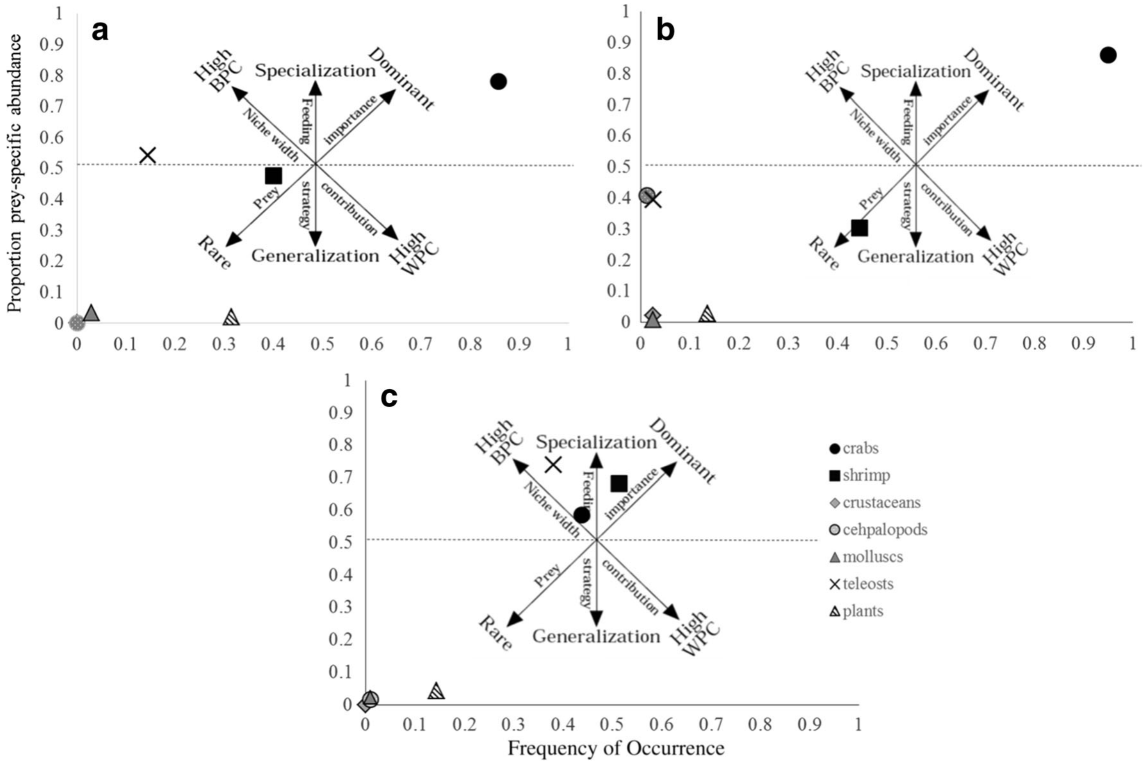

Fig. 4 Prey-importance graphs based on stomach content analysis. Figures follow that of Amundsen et al. 1996 for **a** juvenile bonnetheads, **b** adult bonnetheads, and **c** juvenile red drum. Prey in the *upper right quadrant* indicate dominant prey items that contribute the most to the dietary niche width of the predator whereas prey in the *lower left quadrant* are considered rare prey items and contribute little to the overall dietary niche width

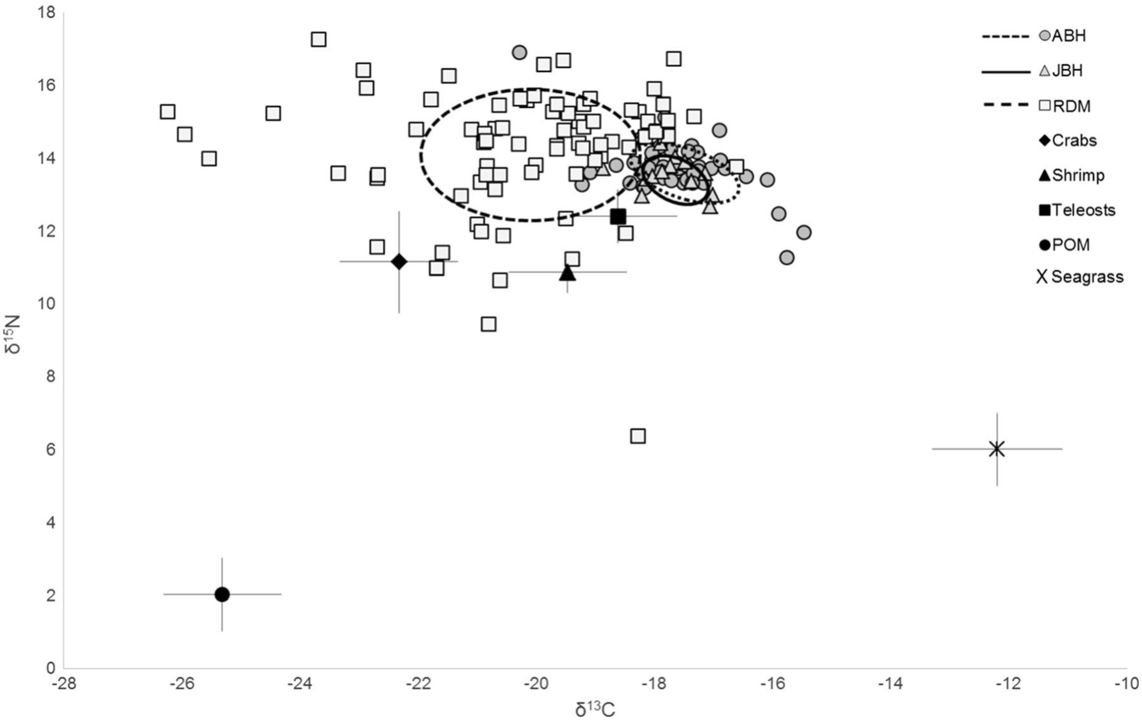

Fig. 5 Stable isotope bi-plot for individual juvenile bonnetheads (*JBH*), adult bonnetheads (*ABH*), and juvenile red drum (*RDM*) based on δ^{13}C and δ^{15}N values. Mean δ^{13}C and δ^{15}N values (±SD) of potential prey items and base values of particulate organic matter (*POM*) are included. SEA_C ellipses are overlaid to show isotopic niche overlap. The overlap among the ellipses represents the degree of shared isotopic niche space by the mesopredators

comprised of different crustacean prey. Differences in consumed prey groups could be attributed to availability of prey, dietary preferences, predator behavior, foraging strategies, or energetic needs (Valiela 1995). Any one or a combination of these factors can lead to resource partitioning that may allow for coexistence of these mesopredators. Differences in habitat use and/or physiological tolerances between these species may also account for differences in the diet trends that we observed. Temperature and salinity have been identified as important factors that drive bonnethead distribution and habitat use (Ubeda et al. 2009; Froeschke et al. 2010, Kroetz et al. 2015). Red drum associate with abiotic and biotic factors in both age- and region-specific ways (Bacheler et al. 2009). Fluctuations in abiotic factors within our study region may have driven differential habitat use by the mesopredators, which could have affected what prey were available for consumption. Changes in mesopredator diversity, abundance, and behavior can also lead to changes in food web dynamics (Ritchie and Johnson 2009; Baum and Worm 2009). Within our study region, other mesopredators were likely present and may have competed for prey resources, which could have contributed to the differences we observed. Both Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) and blacktip sharks (*Carcharhinus limbatus*) inhabit our study area. Both of these species have a diet comprised mainly of teleosts, but they also consume crabs and shrimp within our study region (Hoffmayer and Parsons 2003; Drymon et al. 2012). This potential competition by other mesopredators may have influenced what prey were consumed and observed in our analysis.

We observed considerable differences in red drum and bonnethead dietary diversity. Red drum had significantly lower prey diversity in their diets compared with bonnetheads. The higher prey diversity shown in individual bonnetheads can be attributed to the many different species of crab present in bonnethead stomachs at one time whereas lower dietary diversity in red drum may be due to one species and/or prey category present in stomachs, likely an artifact of stomach content analysis. Intraspecific variation in diet may play a role in reducing interspecific competition within the northern GOM waters. For example, individual dietary preferences and predator behavior may determine what prey are consumed. Juvenile red drum have been shown to exhibit site fidelity to estuarine tidal creeks throughout Mobile Bay (Powers, unpublished data) and similarly, bonnetheads exhibit site fidelity to specific areas in Mississippi Sound (Kroetz et al. 2015). Potential habitat partitioning may have affected what prey were available and consumed by each species. This could have potentially led to reduced competition of the mesopredators allowing both species to consume similar prey items and coexist in the same ecosystem.

If analyzing diet at the population or community level, intraspecific variation and dietary diversity can be lost. Similarly, if only a single metric is used to define trophic relationships, specificity can be lost over temporal scales. For example, there was zero to minimal isotopic niche overlap of red drum with juvenile and adult bonnetheads, respectively; this is similar to what was reported for these two species on the east coast of the USA (Shaw et al. 2016). In contrast, stomach content analysis revealed more dietary overlap than suggested by the stable isotope mixing models. In general, red drum had occupied a greater isotopic niche space than bonnetheads. These differences can be attributed to the different temporal scales of each analysis (i.e., short-term vs. long-term), isotopic values of our potential prey items, or mobility of bonnetheads and red drum.

Defining ecological and dietary specialization for coastal fishes is difficult (Munroe et al. 2014). Specialization can be defined based on a multitude of characteristics, including morphological and dietary strategies (Munroe et al. 2014). For example, bonnetheads could be considered dietary specialists based on morphological and feeding mechanics (Wilga and Motta 2000) as well as from stomach content analysis (Cortés et al. 1996). Our sampled population of mesopredatory bonnetheads and red drum occupied varying niche widths with intraspecific diversity in consumed prey within each population. Resource scarcity can lead to trophic specialization because individual predators that use a narrow range of resources have the potential to be more efficient at exploiting resources (Bolnick et al. 2003). Both life stages of bonnetheads and juvenile red drum overlap spatially and interspecific competition may be a driver of the variation of prey resources that we observed. Intraspecific competition of juvenile and adult bonnetheads may not be as prominent as dietary and isotopic overlap was high, and we observed potential resource partitioning, mainly by adult bonnetheads. Further investigation into the predator-prey interactions of these two mesopredator species will provide the necessary information on inter- and intraspecific competition (Kroetz unpublished data) needed to determine the specific role that juvenile and adult bonnetheads and juvenile red drum play in ecosystem function.

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