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Author: Shaw, Ashley L.

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ARTICLE

Trophic Ecology of a Predatory Community in a Shallow-Water, High-Salinity Estuary Assessed by Stable Isotope Analysis

Ashley L. Shaw*
South Carolina Department of Natural Resources, 217 Fort Johnson Road, Charleston, South Carolina 29412, USA; and Grice Marine Laboratory, Department of Biology, College of Charleston, 205 Fort Johnson Road, Charleston, South Carolina 29412, USA

Bryan S. Frazier
South Carolina Department of Natural Resources, 217 Fort Johnson Road, Charleston, South Carolina 29412, USA

John R. Kucklick
National Institute of Standards and Technology, Organic Chemical Measurement Science Group, Hollings Marine Laboratory, 331 Fort Johnson Road, Charleston, South Carolina 29412, USA

Gorka Sancho
Grice Marine Laboratory, Department of Biology, College of Charleston, 205 Fort Johnson Road, Charleston, South Carolina 29412, USA

Abstract

Estuaries serve as habitats and nurseries for many recreationally and commercially important fishes, often contributing recruits to adult populations that remain in close proximity to estuarine environments. Upper-level predatory fish species are among the most sought after by fisheries; thus, an understanding of the trophic dynamics of the community can assist ecological fisheries management of these highly productive ecosystems. Dietary niche overlap within the predatory fish community of Bulls Bay, a subtropical estuary in South Carolina, was assessed by using stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to compare seven elasmobranch species and three teleost species. Cownose Rays *Rhinoptera bonasus* and Finetooth Sharks *Carcharhinus isodon* had no isotopic overlap with other species and therefore exhibited unique isotopic niche spaces that were indicative of potential resource partitioning. The teleosts and remaining elasmobranchs had varying degrees of overlap, implying shared resources; a high degree of dietary niche overlap was observed among Spotted Seatrout *Cynoscion nebulosus*, Sandbar Sharks *Carcharhinus plumbeus*, and Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae*. Although most pairs of species showed some isotopic overlap, there were also interspecific differences in niche overlap, signifying that this predatory fish community has a widely varied prey base overall. Bulls Bay is an important nursery habitat with a balanced predator community, as illustrated by a combination of unique dietary niches and varying degrees of dietary niche overlap.

South Carolina estuaries are critical habitats for many economically and ecologically important fish species (Wenner et al. 1990; Castro 1993; Blaber et al. 2000; Ulrich et al. 2007), which comprise a predator community similar to

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*Corresponding author: shawa@dnr.sc.gov
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those found in other estuarine waters along the southeastern U. S. and Gulf of Mexico coasts (Moncreiff and Sullivan 2001; Bethea et al. 2004; Lellis-Dibble et al. 2008). Juveniles of teleost species with recreational angling importance utilize shallow tidal creeks and stretches of marsh vegetation in South Carolina estuaries as primary habitat (Wenner et al. 1990). Estuaries in South Carolina serve as communal nurseries for several coastal shark species (Castro 1993; Ulrich et al. 2007), some of which are also important targets of recreational fisheries. The presence of many species at an important stage of growth within a common habitat raises questions about the availability and abundance of resources within estuaries and about whether shared resources may be a cause for competition among co-existing teleosts and elasmobranchs.

Predatory fishes link pelagic and benthic food chains in aquatic systems through trophic interactions (Rooney and McCann 2012; Baustian et al. 2014) and may therefore influence and have a stabilizing effect on the trophic structure of a community or ecosystem (Arim et al. 2010; Rooney and McCann 2012). Little is known about trophic interactions between elasmobranchs and teleosts—which together represent a mid- to upper-level predator community—in South Carolina estuaries (Cortes 1999; Akin and Winemiller 2008). One way to determine a community's connectivity is by studying foraging ecology and dietary overlap (Herzka 2005), which can be used to infer trophic ecology, interspecific competition, and niche partitioning within a community (Newsome et al. 2007).

The traditional method of studying the diets of one or more species is stomach content analysis (SCA). However, SCA for dietary overlap studies often requires the sacrifice of a large number of fish to properly characterize the diets, as was illustrated in previous diet studies conducted using cumulative prey curves (Ferry and Cailliet 1996; Cortes 1997; Hoffmayer and Parsons 2003; Bethea et al. 2004; Torres-Rojas et al. 2010). In addition, SCA results represent only a snapshot of the diet and may not adequately describe the diet in its entirety due to differential digestion of prey and differential food availability (Hyslop 1980; Pinnegar and Polunin 1999).

Stable isotope analysis (SIA) can be a minimally invasive, nonlethal technique (Baker et al. 2004) that provides information on the assimilated diet of an organism, reflecting its previous trophic history. Carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, respectively) are time-integrated measures of diet that reflect long-term foraging by an individual (tissue turnover ranging from ~40 d for juvenile teleosts to ~200–500 d for elasmobranchs and slower-growing teleosts; MacAvoy et al. 2001; Suzuki et al. 2005; MacNeil et al. 2006; Logan and Lutcavage 2010) and the assimilated organic material of a diet rather than a snapshot of the organism's recent prey as determined from traditional SCA (Peterson and Fry 1987; Gannes et al. 1997). The SIA method bypasses the problem of empty stomachs due to regurgitation, the bias of opportunistic feeding, and the confounding effects of differential digestibility of prey items in the stomach (Borrell et al. 2011). The SIA approach is based on the predictive enrichment of $\delta^{13}C$ and $\delta^{15}N$ between a basal source or prey item and a consumer. Carbon isotopic ratios exhibit little enrichment between trophic levels; they primarily reflect basal carbon sources from the benthic or pelagic source upon which an organism is feeding if there are at least two isotopically distinct carbon sources within the ecosystem (Peterson and Fry 1987), thereby providing information about carbon flow in the estuary. Stable nitrogen fractionates to a greater extent between trophic levels and is therefore indicative of an individual's relative trophic position within the ecosystem (DeNiro and Epstein 1981; Minagawa and Wada 1984; McCutchan et al. 2003). In a review of isotopic fractionation values for teleost muscle, Caut et al. (2009) found an average diet–tissue discrimination value of 2.5‰ for nitrogen isotopes and 1.8‰ for carbon isotopes. Elasmobranchs have various fractionation values that, according to recent research, are species specific. For example, Hussey et al. (2010) found a factor of 2.4‰ for nitrogen isotopes and a factor of 0.9‰ for carbon isotopes in the muscle of Sand Tigers *Carcharias taurus*. Kim et al. (2012) reported a fractionation of 3.7‰ for nitrogen isotopes and 1.7‰ for carbon isotopes in the muscle of Leopard Sharks *Triakis semifasciata*.

Fishing pressure and habitat loss threaten the health of estuarine ecosystems and can lead to imbalances in estuarine community structure (Pinnegar et al. 2000; Kennish 2002). Therefore, baseline data are needed to track community changes over time. Studies of competition and dietary niche overlap among shark species are often complicated by these species' generally large sizes, relatively low abundances, and high mobility. However, isotopic data are relatively easy to collect from a large number of individuals and species, particularly within certain estuaries. In the southeastern USA, some shallow-water estuaries, such as Bulls Bay, South Carolina, act as nursery areas for coastal sharks and therefore contain relatively high numbers (i.e., relative to other coastal habitats) of juvenile sharks representing several species, thereby allowing dietary studies to be conducted with relative ease (Papastamatiou et al. 2006). The use of SIA is now common in ecological studies analyzing resource use by fishes, examining food web structure, defining relative trophic positions, and measuring dietary niche breadth of individual fish species and dietary niche overlap between fish species in communities (Layman et al. 2007; Hussey et al. 2012; Shiffman et al. 2012).

Many current and past fisheries management strategies have focused on single-species stock assessment models and have often overlooked the importance of predation and trophic interactions (Latour et al. 2003). Ecosystem-based fishery management is a holistic approach that considers the diets and trophic relationships of several species and prioritizes the ecosystem—rather than a single species—as its focus

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(Pikitch et al. 2004; Levin et al. 2009; Link and Browman 2014). Mid- to upper-level predatory fishes are among the species that are most sought after by commercial and recreational fishers in estuarine systems. Changes in estuarine trophic structure due to fishing pressure heighten the importance of determining the trophic ecology and dietary niches of predatory species to infer interspecific relationships within estuarine fish communities. These trophic data can contribute valuable information for the development of ecosystem-based fisheries management plans.

We examined the trophic ecology of an estuarine-dependent predatory fish community in Bulls Bay (Figure 1) by using SIA to analyze the dietary niche overlap of 10 co-occurring fish species (seven elasmobranchs and three teleosts) and to infer their potential prey. In addition to elucidating important trophic information about each predator species, this study presents trophic connections within the community and explores the possibility of resource sharing, partitioning, or both among the predators.

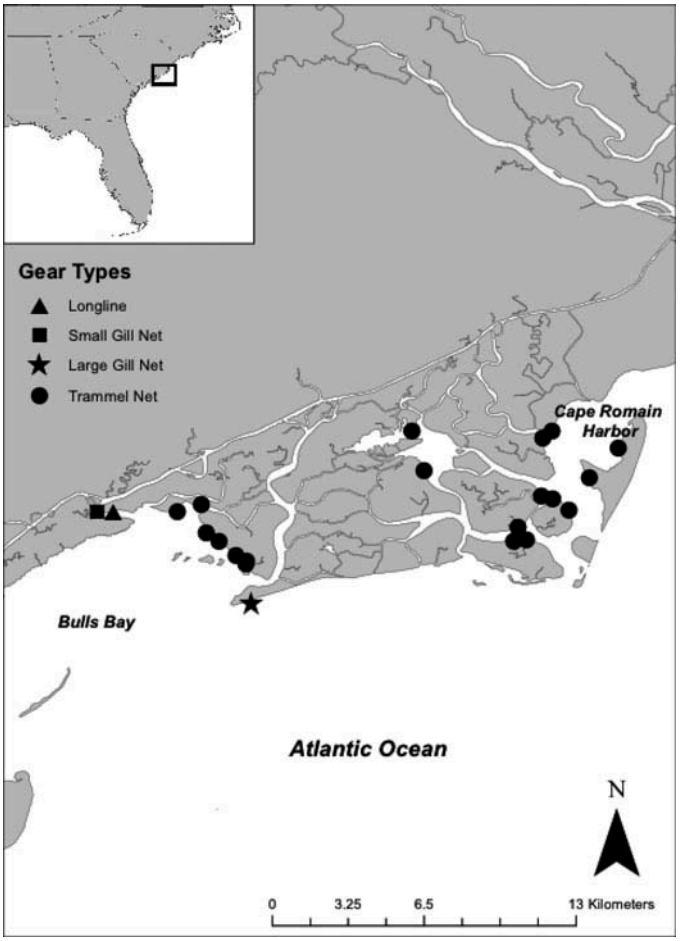

FIGURE 1. Map of sampling locations in Bulls Bay, South Carolina, and surrounding waters. Samples were collected via gill nets and longlines through the Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) survey and via trammel nets through the South Carolina Department of Natural Resources estuarine finfish survey.

METHODS

Study site and sample collection.—This study took place in the Bulls Bay estuarine system, located within the Cape Romain Wildlife Refuge, South Carolina. The estuary has minimal freshwater discharge and is considered a high-salinity, non-salt-wedge estuary (Mathews et al. 1980; Sandifer et al. 1980). It consists of anastomosing small creeks and deeper central channels with shallow mudflats along raised vegetated edges comprised mostly of saltmarsh cordgrass *Spartina alterniflora*.

To perform SIA, we collected muscle tissue samples from seven elasmobranchs (six shark species and one ray species): the Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*, Blacktip Shark *Carcharhinus limbatus*, Bonnethead *Sphyrna tiburo*, Finetooth Shark *Carcharhinus isodon*, Sandbar Shark *Carcharhinus plumbeus*, Scalloped Hammerhead *Sphyrna lewini*, and Cownose Ray *Rhinoptera bonasus*. We also collected samples from three teleost species: Red Drum *Sciaenops ocellatus*, Southern Flounder *Paralichthys lethostigma*, and Spotted Seatrout *Cynoscion nebulosus*. The majority of elasmobranchs sampled were considered young of the year (age 0) or juveniles, with the exception of Bonnetheads and some Atlantic Sharpnose Sharks. To limit maternal influence on the isotopic signatures of elasmobranchs, muscle samples were taken only from sharks with fully healed umbilical scars (Olin et al. 2011). All of the sampled Red Drum and most of the Southern Flounder were considered juveniles, whereas all Spotted Seatrout and some Southern Flounder were of adult size according to the maturity indices of Wenner et al. (1990). Cownose Rays have a specialized diet consisting of bivalve mollusks (Collins et al. 2007; Ajemian and Powers 2011) and were included as an outgroup or reference species to the other predatory fishes in various analyses because their diet differs from the more varied diets of sharks and teleosts, which feed on prey from higher trophic levels. Potential prey taxa were selected from past SCAs conducted on the 10 predator species we analyzed (Wenner et al. 1990; Bush 2003; Bethea et al. 2004; Ellis and Musick 2007); in total, 24 prey species that had been identified as important in the diets of one or more predator species were sampled in Bulls Bay.

Because the species of interest show seasonally changing abundance patterns, samples were only collected between May and early October in 2011 and 2012. Three gear types were used for collecting samples at locations in Bulls Bay: longlines, gill nets, and trammel nets. Elasmobranchs were primarily caught by using a hand-deployed longline and gill nets at fixed stations within Bulls Bay, whereas teleost samples were typically collected by trammel nets that were set adjacent to Bulls Bay (Figure 1).

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Teleost fishes were measured in SL (mm), sharks were measured in FL, and rays were measured in disk width (DW) before being released. Sex was determined for all elasmobranchs; however, sex determination for teleosts required gonad analysis, which only occurred for individuals that were sacrificed for use in other studies. Muscle samples (~60 mg) for SIA were taken from the dorsal musculature with a sterile, 4-mm, disposable biopsy punch (Premier Medical Products Unipunch) and were placed in 2-mL cryovial tubes; upon arrival at the laboratory, the samples were frozen at –80°C until processing.

We collected live saltmarsh cordgrass, live phytoplankton, and surface sediment samples from areas adjacent to predator sampling sites so as to characterize the basal carbon sources of estuarine primary producers. Phytoplankton samples were collected by surface plankton tows, and zooplankton was separated from phytoplankton by viewing the samples under magnification. Sediment samples were collected from the top 2 mm of marsh mud surface that was covered with water; the samples represented a mixture of basal resources available on the sediment (Wright et al. 2014). Mud samples were homogenized and subsampled for use in SIA. The sediment samples were not treated for carbonate reduction, but 17 of the samples were tested to average out the benthic algae signature. In addition, our sediment isotopic signatures were comparable to those observed by Wright et al. (2014) in a Georgia estuary that is very similar to Bulls Bay (dominated by saltmarsh cordgrass, mudflats, and oyster reefs). All materials collected for SIA were frozen at –80°C until processing.

Stable isotope processing.—Samples were thawed, and skin was removed when present. Muscle samples were lyophilized (VirTis Genesis XL25, Wizard 2.0; SP Scientific) for at least 40 h, and the tissue was ground into a fine powder with a bead beater (Mini-Bead Beater 8, BioSpec Products). To reduce sources of error and to standardize the data across multiple species (Hussey et al. 2012), we extracted the lipids by following a modified Bligh and Dyer (1959) method in which approximately 2 mL of 2:1 chloroform: methanol solution were added to each powdered sample. The samples were placed in a warmwater bath, sonicated for 15 min (Fisher-Scientific FS50), and centrifuged (IEC Centra CL3) at 1,200 rotations/min for 5 min; the solvent was extracted from each tube. The process was then repeated. In addition to lipid removal, this method is designed to remove urea from elasmobranch muscle tissue (Christie 1993), which is important because urea in the muscle may misrepresent the isotopic values by exhibiting more depleted $\delta^{13}C$ values relative to those observed when urea is removed (Kim and Koch 2012).

Stable isotope analysis was performed by using a Thermo Flash Elemental Analyzer coupled to a ThermoFisher Scientific Delta V Plus isotope ratio mass spectrometer at the Skidaway Institute of Oceanography's (SKIO) Scientific Stable Isotope Laboratory (SSIL), Savannah, Georgia. Stable isotopes were expressed in delta notation as differences (‰) from a standard,

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000,$$

where R_{sample} refers to the ratio of heavy isotope to light isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$); and $R_{standard}$ is the Pee Dee Belemnite standard for carbon or the atmospheric N_2 standard for nitrogen. Throughout the analysis, chitin powder standards were run as a control for isotopic values ($\delta^{13}C$: mean ± SD = –19.0 ± 0.09‰; $\delta^{15}N$: –1.0 ± 0.09‰; from 2012 samples). The long-term SD (a measure of precision) at SKIO-SSIL is ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ (J. Brandes, SKIO-SSIL, personal communication).

Statistical analysis.—The assumption that data were normally distributed was tested by using a Shapiro–Wilk test for multivariate data. Differences in mean bivariated isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) across all predators were assessed by multivariate ANOVA (MANOVA), which was followed by a univariate ANOVA to evaluate whether differences in isotopic niche space were due to differences in both $\delta^{13}C$ and $\delta^{15}N$. We used post hoc Tukey's honestly significant difference (HSD) tests to group species that exhibited significantly different mean $\delta^{13}C$ and $\delta^{15}N$ values.

Quantitative metrics to assess interspecific comparisons were calculated according to Layman et al. (2007). Metrics (hereafter, "Layman metrics") included the $\delta^{15}N$ and $\delta^{13}C$ range between the most- and least-enriched species; the mean distance to the centroid (CD); the mean nearest-neighbor distance (M-NND); the SD of nearest-neighbor distance (SD-NND); and the mean distance of each individual to all other individuals. The CD represents the average degree of trophic diversity within a species, whereas the M-NND and SD-NND represent the density and evenness, respectively, of species packing within the isotopic niche space.

The standard ellipse area (SEA) for each species was calculated as an estimate of isotopic niche width; we used a corrected SEA (SEA_c), which reduces bias for small sample sizes (Jackson et al. 2011; Syvaranta et al. 2013). Dietary niche overlap was calculated with Stable Isotope Bayesian Ellipses for R (SIBER) using the Stable Isotope Analysis in R (SIAR) package (Parnell and Jackson 2013). To gain insight into food web dynamics, we used the SIAR package's Bayesian mixing models in an attempt to estimate the contribution of carbon source as well as potential prey items for each species. Fractionation values (correction factors in SIAR) between resources and consumers with lipid-extracted samples were assumed to be 1.8 ± 0.65‰ (mean ± SD) for $\delta^{13}C$ and 3.2 ± 0.74‰ for $\delta^{15}N$ based on a meta-analysis by McCutchan et al. (2003). Because there are multiple trophic levels between the basal resources and the predators, these fractionation values were multiplied by 3 (Phillips 2012). Up to 500,000 iterations were used for each species group.

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To determine whether body size was a factor in $\delta^{15}N$ or $\delta^{13}C$ differences between species, linear regressions or nonparametric tests (Kendall's robust line fit method) were used to detect relationships between $\delta^{13}C$ or $\delta^{15}N$ values and size for each predator species. Relationships between isotopic values and capture day were explored to detect possible changes in the diet throughout the summer or to detect maternal influence on isotopic signatures of age-0 elasmobranchs. Placentatrophic neonate sharks have an enriched signature relative to their mothers (Olin et al. 2011). The individuals with isotopic signatures that most likely reflected the maternal signatures (i.e., the earliest-caught age-0 Atlantic Sharpnose Sharks) were removed from analyses. All statistical analyses were performed in R software (R Development Core Team 2010).

RESULTS

Overall, 313 muscle samples for use in SIA were collected from 10 predatory fish species (Table 1). Average $\delta^{13}C$ values of the 10 species ranged from –18.16‰ to –15.82‰ (Table 2). Average $\delta^{15}N$ values spanned a larger range than $\delta^{13}C$ (from 9.42‰ to 15.22‰), indicating that the predators fed on prey across multiple trophic levels. The variance of average isotopic values for individual species was diverse for both $\delta^{13}C$ and $\delta^{15}N$, suggesting the presence of varied feeding strategies in the predator community. Among the apex predators, Scalloped Hammerheads were the most enriched in $\delta^{15}N$ (mean ± SD = 15.22 ± 0.85‰), whereas Red Drum were the least enriched in $\delta^{15}N$ (11.88 ± 0.82‰). Feeding at a lower trophic level than the other predators, Cownose Rays displayed the lowest mean $\delta^{15}N$ value (9.42 ± 0.52‰). Red Drum were the most enriched in $\delta^{13}C$ (–15.82 ± 0.78‰), whereas Finetooth Sharks were the least enriched (–18.16 ± 0.27‰). According to Layman metric values, Finetooth Sharks and Blacktip Sharks had the lowest amount of isotopic variation (Table 2). Among the predators we examined, Finetooth Sharks had the smallest ranges of $\delta^{13}C$ and $\delta^{15}N$ and the smallest CD, M-NND, and SD-NND values; Blacktip Sharks had the next-smallest values for all metrics except M-NND. Overall, across the calculated Layman metrics, the teleost species had more average variation than the elasmobranchs (Table 2).

Relationships between isotopic values and predator size as well as capture day (day of the year) were assessed by use of regression models (Table 3). Species with a significant relationship between only one isotopic ratio and either size or capture day were considered to constitute a single group. Red Drum displayed a linear relationship between size and both of the isotopic ratios. There was a significant difference in $\delta^{13}C$ and $\delta^{15}N$ between length-groups (<400 and ≥400 mm SL) of Red Drum (*t*-test, $\delta^{13}C$: $t = -2.51$, $P = 0.02$; $\delta^{15}N$: $t = -2.81$, $P = 0.007$); however, there was a gap in the data due to a lack of intermediate lengths for Red Drum, and the large amount of variation in the regressions between isotope ratios and fish size resulted in low R^2 values ($\delta^{13}C$: $R^2 = 0.07$; $\delta^{15}N$: $R^2 = 0.15$). Therefore, Red Drum remained as a single group, although we analyzed the size-classes separately to investigate ontogenetic shifts. When analyzed as different length-groups (244–377 and 400–642 mm SL), larger Red Drum were found to have a higher $\delta^{15}N$ signature than smaller fish.

Data for eight of the predator species were normally distributed, but the $\delta^{13}C$ and $\delta^{15}N$ distributions for Atlantic Sharpnose Sharks and Cownose Rays were nonnormal even after multiple data transformations. For the nonnormal data, we used Kendall's robust model (a nonparametric test) to assess the relationship between isotopic values and size or capture day (Table 4). When isotopic data for Atlantic Sharpnose Sharks were divided according to the month of

TABLE 1. Capture dates of predator species in Bulls Bay, South Carolina, expressing the seasonal range of captures (encompasses data from both 2011 and 2012). Sizes are reported in FL for sharks, disk width (DW) for Cownose Rays, and SL for teleosts.

Species	*n*	Males	Females	Size range (mm)	Range of capture dates
Elasmobranchs					
Atlantic Sharpnose Shark	39	28	11	275–799	Jul 10–Sep 28
Atlantic Sharpnose Shark, age 0	18	10	8	275–405	Aug 3–31
Blacktip Shark	19	6	13	474–935	Jul 26–Aug 13
Bonnethead	30	3	27	572–969	May 5–Sep 28
Cownose Ray	29	8	21	430–680	Jul 5–Aug 31
Finetooth Shark	32	8	22	439–663	Jul 26–Aug 17
Sandbar Shark	30	15	15	480–731	Jul 10–Aug 31
Scalloped Hammerhead	37	18	19	318–498	Jul 5–Aug 31
Teleosts					
Red Drum	45	3	6	194–642	Jul 19–Oct 13
Southern Flounder	22	2	NA	153–380	Jul 19–Oct 14
Spotted Seatrout	30	3	2	232–377	Jul 19–Oct 14

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TABLE 2. Layman metrics (Layman et al. 2007) and standard ellipse areas (SEAs) for members of the predator community in Bulls Bay, South Carolina. The second row for Atlantic Sharpnose Sharks refers to the Layman metric and SEA analyses conducted only with data from August-caught age-0 sharks (normally distributed isotopic values), which are referred to here simply as age 0; mean (±SD) and range of $\delta^{15}N$ and $\delta^{13}C$ are also presented (CD = mean distance to the centroid; M-NND = mean nearest-neighbor distance; SD-NND = SD of nearest-neighbor distance; SEA_c = corrected SEA).

Species	Mean $\delta^{15}N$ (‰)	$\delta^{15}N$ range (‰)	Mean $\delta^{13}C$ (‰)	$\delta^{13}C$ range (‰)	CD	M-NND	SD-NND	SEA	SEA_c
Elasmobranchs									
Atlantic Sharpnose Shark	13.80 ± 0.61	2.70	–16.88 ± 0.76	3.72	0.84	0.26	0.26	0.754	0.784
Atlantic Sharpnose Shark, age 0	13.66 ± 0.34	1.14	–17.20 ± 0.79	3.17	0.68	0.31	0.31	0.837	0.890
Blacktip Shark	14.62 ± 0.25	0.90	–16.90 ± 0.45	1.62	0.45	0.19	0.12	0.339	0.359
Bonnethead	12.79 ± 0.26	1.08	–17.09 ± 0.57	2.62	0.51	0.17	0.14	0.440	0.456
Cownose Ray	9.42 ± 0.52	2.13	–18.09 ± 0.56	2.62	0.58	0.21	0.26	0.819	0.849
Finetooth Shark	14.53 ± 0.18	0.74	–18.16 ± 0.27	1.13	0.29	0.09	0.06	0.151	0.156
Sandbar Shark	13.96 ± 0.60	2.40	–16.61 ± 0.66	3.15	0.79	0.21	0.17	1.243	1.288
Scalloped Hammerhead	15.22 ± 0.85	4.65	–16.49 ± 0.60	2.48	0.87	0.29	0.28	1.567	1.612
Teleosts									
Red Drum	11.88 ± 0.82	3.46	–15.82 ± 0.78	4.87	0.96	0.27	0.32	1.927	1.972
Southern Flounder	12.51 ± 0.53	2.04	–17.00 ± 1.55	5.86	1.36	0.39	0.28	2.489	2.613
Spotted Seatrout	13.46 ± 0.50	2.37	–16.51 ± 0.81	3.75	0.78	0.31	0.36	1.257	1.302

TABLE 3. Results of linear regression testing the effects of fish size (FL for sharks, SL for teleosts, or disc width [DW] for rays) and capture day (i.e., day of the year; data were combined across years to depict temporal changes) on $\delta^{13}C$ and $\delta^{15}N$ in the muscle tissue of predators sampled in Bulls Bay estuary.

		Fish size						Capture day					
		$\delta^{13}C$			$\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Species	df	F	r^2	P	F	r^2	P	F	r^2	P	F	r^2	P
Blacktip Shark	17	1.21	0.01	0.29	4.96	0.18	0.04	3.41	0.12	0.08	0.07	–0.05	0.80
Bonnethead	28	0.57	–0.02	0.46	0.85	–0.01	0.36	6.44	0.16	0.02	0.54	–0.02	0.47
Finetooth Shark	30	2.47	0.05	0.13	0.03	–0.03	0.86	0.04	–0.03	0.85	4.24	0.09	0.08
Red Drum	43	4.17	0.07	0.05	8.59	0.15	<0.01	2.75	0.04	0.10	8.62	0.15	<0.01
Sandbar Shark	28	13.81	0.31	<0.001	0.002	–0.04	0.96	7.08	0.17	0.01	0.45	–0.02	0.53
Scalloped Hammerhead	35	3.27	0.06	0.08	3.76	0.07	0.06	18.55	0.33	<0.01	0.14	–0.02	0.70
Southern Flounder	20	0.04	–0.05	0.85	0.85	–0.01	0.37	0.03	–0.05	0.88	0.04	–0.05	0.85
Spotted Seatrout	28	0.59	–0.01	0.45	5.07	0.12	0.03	0.22	–0.03	0.64	1.53	0.02	0.23

TABLE 4. Results of nonparametric Kendall's robust models of Atlantic Sharpnose Sharks and Cownose Rays (for which data were nonnormally distributed), testing the effects of size (FL for sharks; disc width [DW] for rays) and capture day (day of the year; data were combined across years to depict temporal changes) on $\delta^{13}C$ and $\delta^{15}N$ in muscle tissue. Data for Atlantic Sharpnose Sharks represent analyses that were conducted on August-caught age-0 individuals and adults.

		Fish size						Capture day					
		$\delta^{13}C$			$\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Species	df	z	τ	P	z	τ	P	z	τ	P	z	τ	P
Atlantic Sharpnose Shark	25	–0.35	–0.05	0.72	–2.19	–0.30	0.03	2.50	0.36	0.01	–0.19	–0.17	0.70
Cownose Ray	29	–0.89	–0.12	0.37	0.75	0.10	0.45						

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capture, data were normal for age-0 sharks caught during August, whereas data for July-caught age-0 individuals were nonnormal and therefore were removed from analyses. The nonnormal distribution of isotopic signatures could be attributable to the presence of very different size-groups within the sample (i.e., shark pups and adults). In addition, the July-caught age-0 Atlantic Sharpnose Sharks had significant relationships between capture day and both $\delta^{13}C$ and $\delta^{15}N$, suggesting a possible maternal input that reflected the foraging location used by the mothers; therefore, these age-0 signatures were likely enriched in $\delta^{13}C$ and $\delta^{15}N$ relative to the maternal tissues (McMeans et al. 2009; Vaudo et al. 2010; Olin et al. 2011). The assumption of normality was relaxed in analyses for Cownose Rays since they served as the out-group.

There was a significant difference in $\delta^{13}C$ between the 2011 and 2012 sampling years for all species except the Cownose Ray, which had a $\delta^{13}C$ value (mean ± SD) of –17.23 ± 0.95‰ in 2011 and a value of –16.22 ± 0.70‰ in 2012. There were no significant differences in $\delta^{15}N$ between study years for any of the species. Data from both years were combined for all species because (1) a minimum sample size of 30 individuals for isotopic analysis was recommended by Syvaranta et al. (2013), particularly when Bayesian ellipses and mixing models are used; and (2) more robust results were desired.

The average isotopic values of predators had significantly different locations in isotopic niche space (MANOVA: F = 73.1, P < 0.001; Figure 2) due to significant differences in $\delta^{13}C$ and $\delta^{15}N$ among all species (ANOVA, $\delta^{13}C$: F = 32.6, P < 0.001; $\delta^{15}N$: F = 268, P < 0.001). The post hoc Tukey's HSD test separated the 10 predators into four groups with similar $\delta^{13}C$ values and into seven groups with similar $\delta^{15}N$ values (Table 5). Based on $\delta^{13}C$ means, groups 2 and 3 demonstrated considerable overlap and were significantly different from group 1 (Red Drum) and group 4 (Finetooth Shark

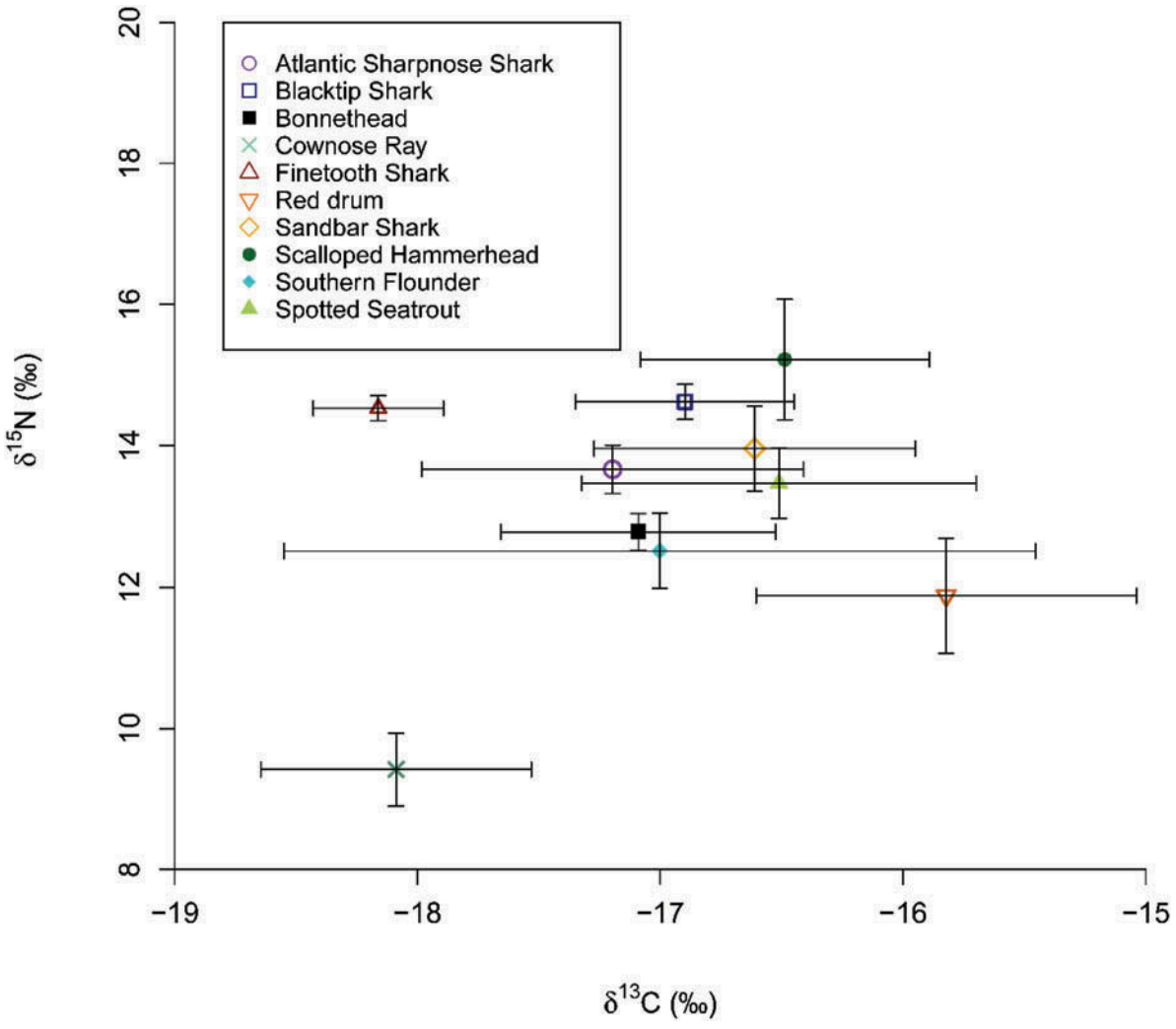

FIGURE 2. Mean (±SD) isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) for elasmobranchs and teleosts belonging to the predator community in Bulls Bay, South Carolina. Only data from age-0 Atlantic Sharpnose Sharks that were caught during August are included in the mean values for that species.

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TABLE 5. Results of post hoc Tukey's honestly significant difference tests, with elasmobranch and teleost species grouped by mean $\delta^{13}C$ values (indicating the range of carbon sources utilized by the predators) and mean $\delta^{15}N$ values (expressing the relative trophic levels of the predators). Asterisks indicate the group (Gr) to which a species belongs.

Species	Mean (‰)	Gr 1	Gr 2	Gr 3	Gr 4	Gr 5	Gr 6	Gr 7
			$\delta^{13}C$					
Red Drum	–15.8	**						
Scalloped Hammerhead	–16.5		**					
Spotted Seatrout	–16.5		**	**				
Sandbar Shark	–16.6		**	**				
Blacktip Shark	–16.9		**	**				
Southern Flounder	–17.0		**	**				
Bonnethead	–17.1		**	**				
Atlantic Sharpnose Shark	–17.1			**				
Cownose Ray	–18.1				**			
Finetooth Shark	–18.2				**			
			$\delta^{15}N$					
Scalloped Hammerhead	15.2	**						
Blacktip Shark	14.6		**					
Finetooth Shark	14.5		**					
Sandbar Shark	14.0			**				
Atlantic Sharpnose Shark	13.5			**	**			
Spotted Seatrout	13.5				**			
Bonnethead	12.8					**		
Southern Flounder	12.5					**		
Red Drum	11.9						**	
Cownose Ray	9.4							**

and Cownose Ray). For the $\delta^{15}N$ means, the only overlap identified by Tukey's HSD test was between group 3 (Sandbar Shark and Atlantic Sharpnose Shark) and group 4 (Spotted Seatrout and Atlantic Sharpnose Shark).

More extensive dietary overlap among species was detected via SIBER analysis when we included all isotopic signatures rather than simply the mean for each species in niche space (Table 6; Figure 3). Finetooth Sharks and Cownose Rays had no dietary niche overlap with any other species. In one instance, the standard ellipses of three species (Spotted Seatrout, Sandbar Shark, and Atlantic Sharpnose Shark) significantly overlapped with each other. Bonnetheads showed the highest overlap, as 98.3% of their standard ellipse overlapped with that of Southern Flounder (Table 6). Overall, dietary niche overlap was slightly less among teleosts than among sharks; the highest area of overlap was observed between Red Drum (33.6% of total isotopic niche area) and Southern Flounder (25.4% of total isotopic niche area). Red Drum and Spotted Seatrout exhibited no dietary niche overlap. In comparison, 41.0% and 20.9% of the ellipse for Blacktip Sharks overlapped with the Scalloped Hammerhead ellipse and the Sandbar Shark ellipse, respectively. Overlap in the ellipses of Atlantic Sharpnose Sharks and Sandbar Sharks constituted 42.7% of the Atlantic Sharpnose Shark ellipse and 29.5% of the Sandbar Shark ellipse.

There were two main carbon resources upon which the predator community relied: phytoplankton and benthic carbon (Appendix Table A.1). Finetooth Sharks and Cownose Rays had isotopic signatures very similar to those of phytoplankton, suggesting that those predators relied heavily on the planktonic food web. Some of the Red Drum had $\delta^{13}C$ values similar to those of saltmarsh cordgrass; however, this carbon source was probably not as important to the diets of the other fish species. The majority of predator isotopic means were most similar to sediment or benthic carbon isotopic values. We collected a total of 116 muscle samples across 24 potential prey species (Table A.1). In general, the isotopic signatures of the potential prey items (6 invertebrate species and 18 teleost species) were intermediate between the $\delta^{15}N$ values of the secondary consumers and the basal resources (i.e., they occupied the isotopic niche space that would be expected for primary consumers in a food web).

DISCUSSION

An understanding of food web structure and resource use in an ecologically and economically important ecosystem is necessary to comprehend the trophic structure of communities. In addition, knowledge of a community or ecosystem's trophic ecology is necessary for detecting changes in trophic structure

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TABLE 6. Percentage overlap in standard ellipses (determined using the corrected standard ellipse area) between each pair of predator species. The table is to be read across each row; for example, 35.7% of the Atlantic Sharpnose Shark ellipse overlaps with the Sandbar Shark ellipse, and 21.9% of the Sandbar Shark ellipse overlaps with the Atlantic Sharpnose Shark ellipse. Isotopic values of all Atlantic Sharpnose Sharks combined were nonnormally distributed, but data for August-caught age-0 individuals were normally distributed.

Species	ASN	ASN, age 0	BT	BH	RB	FT	SO	SB	SH	PL	CN
Atlantic Sharpnose Shark (ASN)	–							35.7			59.7
Atlantic Sharpnose Shark, age 0		–						42.7			47.1
Blacktip Shark (BT)			–					20.9	41.0		
Bonnethead (BH)				–						98.3	5.0
Cownose Ray (RB)					–						
Finetooth Shark (FT)						–					
Red Drum (SO)							–			33.6	
Sandbar Shark (SB)	21.9	29.5	5.9					–	5.3		44.3
Scalloped Hammerhead (SH)			9.1					4.2	–		
Southern Flounder (PL)				17.2			25.4			–	0.6
Spotted Seatrout (CN)	35.9	32.2		1.8				43.5		1.2	–

that can occur due to natural effects (e.g., population shifts or localized species die-offs due to temperature intolerance) or anthropogenic effects (e.g., fishing or development). Use of SIA allows researchers to gain trophic information on a complicated estuarine food web—information that would otherwise be taxing to obtain via traditional diet study methods, such as SCA (which requires sacrificing the animal) or gastric lavage.

Varying degrees of isotopic niche overlap among the predators were detected with SEAs, as is expected with a relatively limited isotopic range. However, many species within the community had a large amount of unique isotopic niche space—that is, isotopic space within an ellipse that did not overlap with another species' ellipse. We attributed this result to differences in $\delta^{15}N$ values, suggesting resource partitioning. Red Drum, Finetooth Sharks, and Cownose Rays had large areas of unique isotopic niche space, indicating possible instances of resource partitioning. Red Drum relied more heavily on a saltmarsh cordgrass-based food web (defined by more enriched $\delta^{13}C$ values; Peterson and Fry 1987; Wright et al. 2014), and a large proportion of the diet was likely contributed by Atlantic marsh fiddler crabs (Wenner et al. 1990). Finetooth Sharks and Blacktip Sharks had the tightest clustering of isotopic signatures (M-NND and SD-NND) and the smallest CD values, which suggested a specialized diet (Layman et al. 2007). Both of those shark species are considered to be piscivorous feeders (Bethea et al. 2004), and this was confirmed by their stable isotope values. Finetooth Sharks and Blacktip Sharks had very similar $\delta^{15}N$ ranges, but their $\delta^{13}C$ values were distinct, suggesting dietary resource partitioning between the two species. Finetooth Sharks and Cownose Rays relied almost strictly on the planktonic food web (specified by the less-enriched $\delta^{13}C$ values; France 1995). Cownose Rays are known to feed heavily on filter-feeding bivalve mollusks (Smith and Merriner 1985; Ajemian and Powers 2011); therefore, the Cownose Ray provided a good reference for the planktonic food web. The diets of Finetooth Sharks within Gulf of Mexico estuaries included a very high proportion of planktivorous Atlantic Menhaden (June and Carlson 1971; Hoffmayer and Parsons 2003; Bethea et al. 2004), and this finding is supported by our SIA results. Evidence of resource partitioning was found during two other community stable isotopic studies: one study was focused on elasmobranch mesopredators (Vaudo and Heithaus 2011), and the other study included predatory elasmobranchs and teleosts (Kinney et al. 2011). Thus, such partitioning may be common when relatively large predator communities co-exist within a habitat.

The small range of average $\delta^{15}N$ values (3.3‰) for predatory fishes indicated that the predator community of Bulls Bay fell within a single trophic level, similar to the results of other community studies in which coexisting species showed high degrees of overlap in stable isotope values (Kinney et al. 2011; Vaudo and Heithaus 2011). However, if we consider all of the sampled individuals, Bulls Bay has a higher trophic diversity with less overlap in $\delta^{15}N$ values relative to those previous studies. The only groups without significantly different mean values of $\delta^{15}N$ from each other included Sandbar Sharks, Atlantic Sharpnose Sharks, and Spotted Seatrout. These three species have similar feeding habits and consume a mixed diet that includes invertebrate and teleost prey (Wenner et al. 1990; Gelsleichter et al. 1999; Bethea et al. 2004; Ellis and Musick 2007), which would place them at similar trophic positions.

Although the mean $\delta^{15}N$ values of all predators fell within the $\delta^{15}N$ range of a single trophic level, the species did not necessarily occupy the same trophic level of the food web. The isotopic signatures of Cownose Rays could be used as a trophic position reference due to their strict diet of bivalve mollusks (Collins et al. 2007; Ajemian and Powers 2011),

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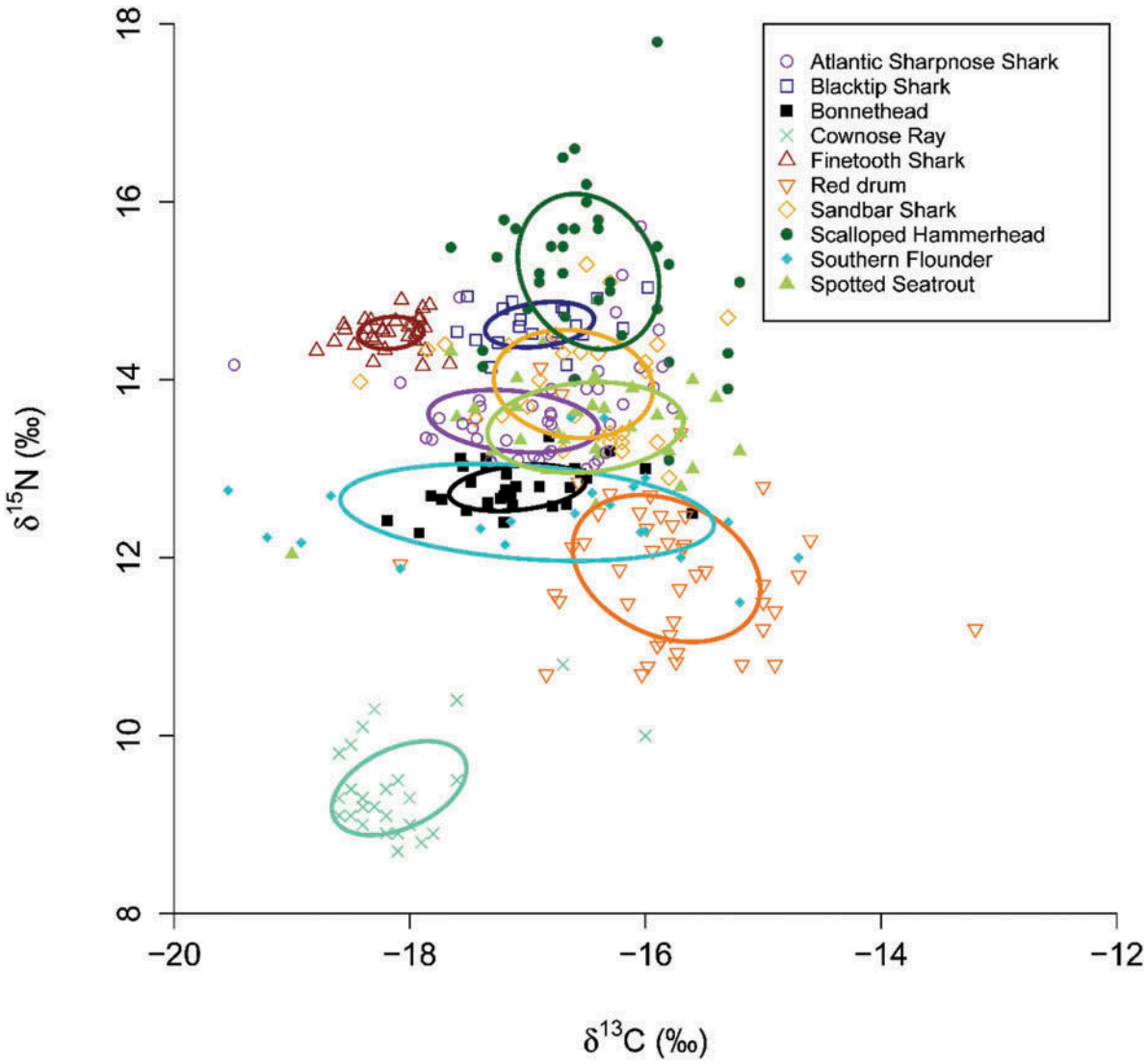

FIGURE 3. Dietary niche overlap for 10 predator species in Bulls Bay, South Carolina. The lines enclose areas that represent each species' corrected standard ellipse area, which was calculated with the program SIBER. The overlap between ellipses represents the degree of shared resource use by two species. Although all sampled individuals are represented on the isotopic biplot, the ellipse for Atlantic Sharpnose Sharks was calculated based on only the August-caught age-0 fish and adults, as those data were normally distributed. The ellipse for Cownose Rays was calculated with nonnormally distributed data, whereas data from the other eight species had normal distributions.

which occupy a basal trophic level as planktonic filter feeders (Moncreiff and Sullivan 2001). The teleosts and other elasmobranch species do not consume a significant amount of mollusks and therefore occupy higher positions within the estuarine food web. Red Drum and Bonnetheads were a slight step up in the trophic food web because they consume large proportions of crustaceans—mostly Atlantic marsh fiddler crabs (Red Drum) and blue crabs (Bonnetheads; Wenner et al. 1990; Cortes et al. 1996; Bethea et al. 2011)—which have slightly more enriched $\delta^{15}N$ values than bivalves (Sullivan and Moncreiff 1990). Blue crabs and Atlantic marsh fiddler crabs were sampled for SIA, and their isotopic signatures fell about one trophic level below those of the Bonnetheads and Red Drum, respectively. Slightly higher above Red Drum and Bonnetheads in isotopic niche space were the predators that consume mixed diets of crustaceans and teleosts: such predators included Southern Flounder, Spotted Seatrout (Wenner et al. 1990), Atlantic Sharpnose Sharks (Hoffmayer and Parsons 2003), and Sandbar Sharks (Ellis and Musick 2007). Higher still were the predominantly piscivorous fish, such as Finetooth Sharks and Blacktip Sharks (Bethea et al. 2004; Barry et al. 2008), which displayed the most enriched $\delta^{15}N$ values (Davenport and Bax 2002).

The teleosts as a group had a diverse diet, as suggested by their fairly high CD values and high variances in $\delta^{13}C$ values (Layman et al. 2007); this observation is in agreement with the

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results of SCA (Wenner et al. 1990). Spotted Seatrout and Southern Flounder appeared to consume a variety of prey species with similar trophic positions, as indicated by their relatively small $\delta^{15}N$ range; in contrast, the larger $\delta^{15}N$ range for Red Drum suggested that they fed on prey across different trophic levels, such as Atlantic marsh fiddler crabs, shrimp, and teleosts (Wenner et al. 1990). Overall, the intermediate to high variances in $\delta^{13}C$ and CD values for Scalloped Hammerheads, Sandbar Sharks, and Atlantic Sharpnose Sharks suggested that these species have also adopted a generalist feeding strategy in Bulls Bay, similar to the results of previous SCAs (Hoffmayer and Parsons 2003; Ellis and Musick 2007; Bethea et al. 2011).

Individuals or species with intermediate $\delta^{13}C$ values may have mixed diets across food webs (feeding on pelagic and benthic prey) or may specialize on prey from the benthic food web (Fry and Sherr 1984). The majority of the predator community (excluding Red Drum, Finetooth Sharks, and Cownose Rays) shared similar basal resources, as indicated by two largely overlapping groups detected by Tukey's HSD test, which separated the species based on their $\delta^{13}C$ values. Spotted Seatrout, Southern Flounder, Sandbar Sharks, Blacktip Sharks, Atlantic Sharpnose Sharks, Bonnetheads, and Scalloped Hammerheads had similar isotopic values that were associated with estuarine sediment values. These seven species could be exploiting a sediment-based food web or could be feeding on a diversity of prey spanning multiple food webs, which appears as a benthic-oriented diet in isotopic niche space (Bearhop et al. 2004).

The small $\delta^{13}C$ range across the community implies that the predators were probably not feeding from the full potential breadth of basal resources within the area. It is possible either that (1) limited carbon sources support the predator community (Layman et al. 2007) or (2) we did not sample all of the carbon sources within Bulls Bay. Since estuaries are mixed bodies of water and since terrestrial and marine carbon resources mix with those found in the estuary (Leakey et al. 2008), gathering the distinct carbon signatures of different food web bases is difficult, and a single isotopic sample may contain multiple basal resources (e.g., a phytoplankton sample may contain saltmarsh cordgrass detritus as well). Because of the difficulty in distinguishing specific carbon resources (i.e., extricating microphytobenthos from the benthic samples or separating saltmarsh cordgrass from the suspended particulates), the sampled sources most likely did not represent the full breadth of food sources for lower-trophic-level organisms within the Bulls Bay estuary. Therefore, our results regarding the importance of particular carbon sources in predator diets are only indicative.

To incorporate age-0 elasmobranchs in an isotopic community study, we found it necessary to examine issues associated with interpreting the isotopic ratios of young sharks. There are three main factors that can confound SIA and the interpretation of isotopic values for age-0 and juvenile individuals of species (particularly elasmobranchs) that live only part of their life in the estuary. These interrelated factors include (1) variation in isotopic signals between estuarine and coastal or offshore waters, which can affect the interpretation of isotopic signatures from species that leave the estuary over the winter (Hobson 1999; Leakey et al. 2008; Shiffman et al. 2014); (2) tissue turnover, which is species specific and can affect the interpretation of isotopic signatures for age-0 individuals and migrating species (Logan and Lutcavage 2010; Olin et al. 2011); (3) inherent isotopic variation; and (4) maternal influence on the isotopic signatures of age-0 fish, which may affect the interpretation of those signatures (Olin et al. 2011).

Estuarine isotopic ratios exhibit depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values in comparison with marine isotopic ratios (McClelland et al. 1997; Leakey et al. 2008); this can be of use to infer whether the tissues of predators truly reflect their estuarine diet. In the present study, teleost isotopic signatures reflected an estuarine isotopic baseline, as the fish remained in the estuary year-round (Wenner et al. 1990). The isotopic signatures for the elasmobranch species, which leave the estuary for coastal and offshore waters when water temperatures decline, showed similar or more depleted $\delta^{13}C$ values than the signatures for teleosts. This finding suggests either that (1) coastal/offshore influences on isotopic signatures due to migration are minimal or (2) muscle tissue turnover in neonates and juveniles is fairly quick.

Although the range of estuarine isotopic ratios is distinct from those of marine and freshwater ratios (Peterson and Fry 1987), the isotopic structure of estuaries can be complex due to mixed diets and opportunistic feeding by predators and due to multiple organic matter sources (Peterson et al. 1985, 1994). In addition, estuaries have changing values of dissolved inorganic carbon (Peterson 1999) and physical mixing, such as bioturbation, which causes sediments at various depth levels to become mixed and to be suspended in the water column and therefore mixed with pelagic carbon (Ember et al. 1987). Due to these complexities, mixing models for the present study were considered unsuccessful in estimating the importance of carbon sources or potential prey items for the predators in Bulls Bay.

Tissue turnover rate and isotopic discrimination factors are species specific and can vary for a number of reasons, including diet type and diet isotope ratios, growth rate, and metabolic processes (McCutchan et al. 2003; Caut et al. 2009). It is preferable to use species-specific values for studies, although the extensive data required for all species are lacking. The discrimination values used for the current study were selected from the study by McCutchan et al. (2003), who provided potentially average discriminated factors across $\delta^{13}C$ and $\delta^{15}N$ for the 10 predator species. The tissue turnover rate in juvenile Sandbar Sharks was shown to begin reflecting a new diet (i.e., diverging from the maternal signature) with a half-life of about 80–100 d for $\delta^{15}N$ and about 130–180 d for $\delta^{13}C$ (Logan and Lutcavage 2010). Malpica-Cruz et al. (2012)

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studied neonate and age-0 Leopard Sharks and reported that muscle tissue turnover took approximately 192 d to reach equilibrium with the diet. Leopard Sharks have low metabolic rates, and their metabolic turnover contributed considerably to isotopic turnover (Malpica-Cruz et al. 2012). Therefore, muscle turnover in age-0 fish adapted to fast swimming with higher metabolic rates could be faster due to a more rapid growth rate in addition to metabolic tissue replacement (Trueman et al. 2005; Carleton and Martinez del Rio 2010; Weidel et al. 2011). The most rapid growth period for sharks occurs at the age-0 and early juvenile stages, when sharks use estuaries as nurseries (Branstetter 1987; Hoenig and Gruber 1990). The teleost species and some of the shark species (e.g., Atlantic Sharpnose Shark) examined in the current study have a rapid early growth rate (Wenner et al. 1990; Loefer and Sedberry 2003) and therefore are likely to exhibit a higher tissue turnover rate than adult sharks. However, if the tissue turnover rates of the age-0 sharks in this study were comparable to those of adult sharks, then their isotopic signatures should be interpreted with caution and may not fully reflect their current diet (Belicka et al. 2012).

It is important to be mindful of inherent isotopic variation within a population when interpreting results that focus on differences in variation, such as dietary niche overlap. A repeated analysis of four subsamples per individual showed that muscle samples from the same individual varied by an average of 0.11‰ for $\delta^{13}C$ and by an average of 0.19‰ for $\delta^{15}N$ (averages derived from three species: the Scalloped Hammerhead, Finetooth Shark, and Atlantic Sharpnose Shark).

Although the predators were analyzed as a single group across years to maintain sample size robustness, the interannual difference in $\delta^{13}C$ may affect interpretation of the proportion of carbon sources that are important to a predator's diet. The shift in $\delta^{13}C$ values across the sampling years may be attributable not to changes in predator diets or prey diets but rather to environmental changes in carbon composition. A shift in the predominance—and therefore the importance—of carbon sources in the estuary and/or the amount of carbon mixing involved could have been caused by a large difference in water temperature: January temperature averaged 6.5°C in 2011 and 11.5°C in 2012 (USGS 2013). Rainfall could have also slightly affected carbon sources; the estimated precipitation during the year preceding the 2011 sampling period was much higher than the estimate for the year preceding the 2012 sampling period (Northeast Regional Climate Center 2015). With slightly less rain in 2012, perhaps the estuary received a larger marine influence (with less freshwater runoff) during that year and therefore had more enriched $\delta^{13}C$ values, since the estuarine environment is depleted in ^{13}C relative to the marine environment (McClelland et al. 1997).

Our results indicated that even though the overall predatory fish community of Bulls Bay has relatively low trophic diversity, there is high variability in species-specific trophic diversity. Some species displayed large or completely unique isotopic niche spaces, indicating potential resource partitioning. Other species demonstrated dietary niche overlap as well as some unique niche space, which showed that they shared prey types with certain community members but also consumed distinctive prey items. Varying degrees of isotopic niche overlap among the predators with a relatively limited isotopic range across the community indicated possible functional redundancy (i.e., distinct species exhibiting similar functional roles [in terms of diet] in an ecosystem). Ecosystems with a higher functional redundancy are more stable and more resilient to changes in community structure, such as a reduced population of a given species (Lundberg and Moberg 2003). Additional research on stomach contents integrated with SIA of these predators would (1) help to clarify the trophic relationships among the predator species and between the predators and their prey and (2) allow exploration of individual dietary specialization within species.

Combining trophic information across multiple species inhabiting an area, their movements within that area, and environmental factors provides a comprehensive view of the ecosystem and a better understanding of how the animals are trophically and spatially connected to each other as well as to the environment. Consumption of prey from different food webs within an ecosystem allows predators to exploit different energy channels, possibly leading to a stabilizing effect on the community and ecosystem (Arim et al. 2010; Rooney and McCann 2012). Fishing pressure or natural disruptions of community structure may upset the stability of the estuarine food web. Our data contribute to baseline information about the trophic relationships within an ecologically and economically important estuarine community; such information is necessary to detect any future changes in trophic structure. Our results demonstrate that due to the interconnectedness of the species within a community, obtaining an understanding of a single species' trophic ecology within an estuary is not necessarily the best strategy to support the management of that species. It is vital to study not only the species of interest but also how those species interact with other members of their community, their prey, and their environment. This highlights the importance of gathering important communitywide trophic information, particularly when designing an ecosystem-based management plan.

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Appendix: Summary of Additional Stable Isotope Information

TABLE A.1. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values for potential prey taxa and basal carbon resources used by the predator community in Bulls Bay, South Carolina.

Species or resource	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Teleosts			
Bay Anchovy *Anchoa mitchilli*	5	–17.73 ± 0.38	12.45 ± 0.30
Silver Perch *Bairdiella chrysoura*	5	–16.57 ± 0.40	12.47 ± 0.15
Atlantic Menhaden *Brevoortia tyrannus*	5	–18.14 ± 0.55	11.18 ± 0.32
Weakfish *Cynoscion regalis*	4	–17.41 ± 0.37	12.85 ± 0.45
Mummichog *Fundulus heteroclitus*	5	–16.17 ± 0.29	11.89 ± 0.31
Pinfish *Lagodon rhomboides*	4	–17.13 ± 0.30	11.78 ± 0.35
Spot *Leiostomus xanthurus*	5	–18.29 ± 0.56	11.29 ± 0.38
Atlantic Silverside *Menidia menidia*	5	–17.24 ± 0.13	12.17 ± 0.10
Southern Kingfish *Menticirrhus americanus*	5	–16.71 ± 0.88	12.97 ± 0.23
Atlantic Croaker *Micropogonias undulatus*	5	–17.54 ± 0.53	12.73 ± 0.58
Striped Mullet *Mugil cephalus*	5	–19.30 ± 4.26	9.60 ± 0.68
Oyster Toadfish *Opsanus tau*	5	–17.88 ± 0.44	12.40 ± 0.39
Harvestfish *Peprilus paru*	4	–18.53 ± 0.53	13.50 ± 1.05
Bighead Searobin *Prionotus tribulus*	2	–16.50 ± 0.02	11.69 ± 0.04
Star Drum *Stellifer lanceolatus*	5	–17.46 ± 0.17	11.80 ± 0.15
Blackcheek Tonguefish *Symphurus plagiusa*	5	–17.59 ± 0.74	11.41 ± 0.12
Atlantic Cutlassfish *Trichiurus lepturus*	2	–17.54 ± 0.13	13.79 ± 0.31
Hogchoker *Trinectes maculatus*	5	–17.17 ± 1.34	12.28 ± 0.33
Invertebrates			
Blue crab *Callinectes sapidus*	7	–15.32 ± 1.00	9.28 ± 0.66
White shrimp *Litopenaeus setiferus*	7	–16.28 ± 0.35	9.56 ± 0.21
Atlantic brief squid *Lolliguncula brevis*	5	–16.67 ± 1.38	12.93 ± 0.41
Daggerblade grass shrimp *Palaemonetes pugio*	9	–16.09 ± 0.82	9.99 ± 0.56
Mantis shrimp *Squilla empusa*	2	–16.74 ± 1.01	10.57 ± 0.10
Atlantic marsh fiddler crab *Uca pugnax*	5	–16.39 ± 0.62	6.93 ± 0.24
Basal resources			
Phytoplankton	5	–18.7 ± 0.6	6.2 ± 0.3
Sediment	17	–16.7 ± 1.2	6.0 ± 1.2
Saltmarsh cordgrass *Spartina alterniflora*	6	–14.4 ± 0.3	6.5 ± 0.7

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