Foraging ecology of large pelagic fishes in the US South Atlantic: structured piscivory shapes trophic niche variation

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ABSTRACT: Sustainable management of marine fishery resources requires an understanding of the ecological relationships that contribute to community structure and population dynamics. In offshore marine ecosystems, the functional roles played by many large pelagic predators are poorly understood, yet this knowledge is essential to ecosystem-based management approaches. Here we report on the results of a multiyear (2010–2013) study to evaluate the trophic relationships within a guild of apex predatory fishes in the western Atlantic Ocean. Quantitative diet analyses were completed for wahoo *Acanthocybium solandri*, dolphinfish *Coryphaena hippurus*, yellowfin tuna *Thunnus albacares*, and blackfin tuna *T. atlanticus* during multiple seasons. Fishes were the most important prey by mass for all predators during all seasons and occurred with high frequency; however, crustacean and molluscan prey were also important dietary components for most of the predators. The diversity of prey eaten was high, with nearly 50 unique families represented; yet, a few prey groups such as scombrid fishes (*Auxis* spp.), flying fish (exocoetids), and ommastrephid squids, occurred more universally and dominated the diets of some predators during certain seasons. Diet similarity was highest between dolphinfish and blackfin tuna and also between wahoo and yellowfin tuna, but was generally dependent on season and driven by overlap in fish prey. Importantly, the extent of piscivory and specialization on unique fish prey groups supported a structured piscivore guild within this pelagic ecosystem, leading to separation among trophic niches and reduced overlap in prey resources. Our findings provide a temporally (seasonal and inter-annual) extensive evaluation of the trophic relationships among large pelagic fish predators in the US South Atlantic, which should inform an ecosystem-based understanding of community dynamics and fishery impacts.

KEY WORDS: Blackfin tuna · Yellowfin tuna · Wahoo · Dolphinfish · Trophic interactions · Predator–prey · Food habits · Trophic niche

1. INTRODUCTION

Understanding species interactions and community dynamics in marine ecosystems is challenging but crucial to supporting ecosystem-based management and conservation (Botsford et al. 1997, Pauly et al. 2000, Francis et al. 2007, Patrick & Link 2015). Our ability to assess the structure, function, and health of global oceans is becoming increasingly complicated as ecosystems undergo unprecedented changes in climate that are shifting how, where, and when species exist and interact

across seascapes (Blois et al. 2013, Poloczanska et al. 2013, Kleisner et al. 2017). These changes, coupled with other historical stressors such as fishing pressure, are acting to alter predator–prey and competitive relationships in varying and idiosyncratic ways that are dependent on species responses to altered environmental conditions and harvest rates with important consequences on system productivity (Pecl et al. 2017, Hobbs et al. 2018). Ecosystem models, such as Ecopath with Ecosim (Colléter et al. 2015) and Atlantis (Olsen et al. 2016), as well as multivariate statistical techniques (e.g. Olson et al. 2014, Duffy et al. 2015, 2017, Bird et al. 2018) that capture simultaneous variation in spatial and temporal patterns among multiple species are becoming increasingly common and reliable tools to investigate broad-scale scenarios of past and future system dynamics under different environmental and management regimes. These models rely heavily upon and are strengthened by high resolution and quantitative information on species foraging ecology, especially data collected concurrently from multiple species (Hollowed et al. 2000, Cox et al. 2002, Jurado-Molina et al. 2005). Current and detailed baseline diet data collected from species of interest is necessary to support ecosystem-based management and to characterize risk associated with changes in climate, fishing pressure, and other stressors (Larkin 1996, Cury et al. 2000, Link et al. 2002, Murawski et al. 2009).

Highly migratory, large pelagic fishes, such as tunas, billfishes, and sharks, inhabit global offshore ecosystems and are known to be highly influential predators capable of structuring community dynamics (Cox et al. 2002, Essington et al. 2002, Myers & Worm 2003). Many of these fishes are opportunistic generalists with high energetic demands and, as such, are responsive to changing prey communities, often adjusting their distribution and foraging behavior in response to local patterns of prey abundance (Ménard et al. 2006, Merten et al. 2014, Duffy et al. 2017). Several members of the large pelagic fish guild also support highly valuable commercial, recreational, and/or artisanal fisheries throughout their global range in tropical, sub-tropical and temperate oceans (ICCAT 2016, Olson et al. 2016). In some global regions (e.g. Pacific Ocean), the trophic ecology and population dynamics of pelagic species have been relatively well studied; however, detailed information on foraging ecology is lacking in the Northwest Atlantic Ocean (NWA), and data are particularly sparse for

small tunas (Dragovich 1969, Manooch & Mason 1983, Rudershausen et al. 2010, Teffer et al. 2015, ICCAT 2016).

Yellowfin tuna *Thunnus albacares*, blackfin tuna *T. atlanticus*, wahoo *Acanthocybium solandri*, and dolphinfish *Coryphaena hippurus* represent a guild of predatory fishes occupying the offshore pelagic ecosystem of the US South Atlantic Bight within the greater NWA. Yellowfin tuna, wahoo, and dolphinfish are routinely harvested by both commercial and recreational fisheries, while blackfin tuna have been mainly targeted by recreational anglers. In recent decades, landings for yellowfin tuna, as well as other large tunas (bluefin *T. thynnus* and bigeye *T. obesus*), have experienced major declines in the Atlantic Ocean, and recent assessments have categorized the Atlantic yellowfin population as overfished (ICCAT 2016). Simultaneously, dolphinfish landings have risen exponentially, both in NWA waters and globally, since the 1950s (Whoriskey et al. 2011, ICCAT 2016, NOAA 2016). Although commercial landings of blackfin tuna and wahoo are considerably lower than yellowfin tuna and dolphinfish, these 2 species are increasingly being targeted in the South Atlantic Bight (NOAA 2016) as well as in other parts of their range (e.g. Pacific Ocean, Perelman et al. 2017; Gulf of Mexico, Cornic & Rooker 2018). However, several aspects of their life history, demography, and ecology in this region are either poorly known or considerably dated (Manooch & Hogarth 1983, Franks et al. 2007, McBride et al. 2008). The status of blackfin tuna populations, in particular, is unknown since no stock assessments or management plans currently exist for this species (ICCAT 2016). Tunas, wahoo, and dolphinfish often co-occur, suggesting that they rely on similar food and habitat resources; nonetheless, each species possesses unique morphological and behavioral characteristics as well as thermal habitat and depth preferences that may contribute to differences in resource utilization and ecological niches (Kleisner et al. 2010).

To help elucidate trophic roles, fill major knowledge gaps, and support the implementation of ecosystem-based management approaches, this study quantified several aspects of the foraging ecology of 4 sympatric pelagic fish species — blackfin tuna, yellowfin tuna, dolphinfish, and wahoo — in the US South Atlantic Bight region. A temporally extensive (multiple years and seasons) analysis of stomach contents was used to demonstrate interspecific, ontogenetic, and seasonal patterns of prey use. Predator–

prey body size relationships were quantified to examine size-based foraging patterns and inform trophic niche breadth. Estimates of dietary overlap were generated to assess the potential for competition among the 4 predators, and multivariate analyses were used to identify patterns of similarity as well as sources of dissimilarity in predator trophic ecology.

2. MATERIALS AND METHODS

2.1. Sample collection

Fishes caught by commercial and recreational fishermen in the offshore waters of North and South Carolina were sampled over a 4 yr period between 2010 and 2013. Sampling was concentrated during spring through fall (April to October) because of the high amount of recreational fishing effort during this period. State and privately organized fishing tournaments were the primary source of fish during the warmer months. During winter and early spring (January to March), samples were obtained from a combination of commercial and recreational/charter fishing fleets. No samples were collected during November or December due to the low incidence of fishing activity. For all recreational landings, fishing occurred during daylight hours in waters over the outer continental shelf, the shelf-slope break, and the Gulf Stream Current, roughly between latitudes 31.5° and 36.25° N (Fig. 1). All fish were caught using hook and line gear by trolling ballyhoo *Hemiramphus brasiliensis*, mullet (Mugilidae), Spanish mackerel *Scomberomorus maculatus*, other bait, or artificial lures. Capture time and the specific gear used for commercially landed fish was not recorded, but fish were primarily captured using hook and line gear with electric or hydraulic reels (e.g. bandit rigs). All fish were sampled dockside and measured as curved fork length (CFL) to the nearest mm; stomachs were then removed, placed on ice and frozen upon return to the laboratory.
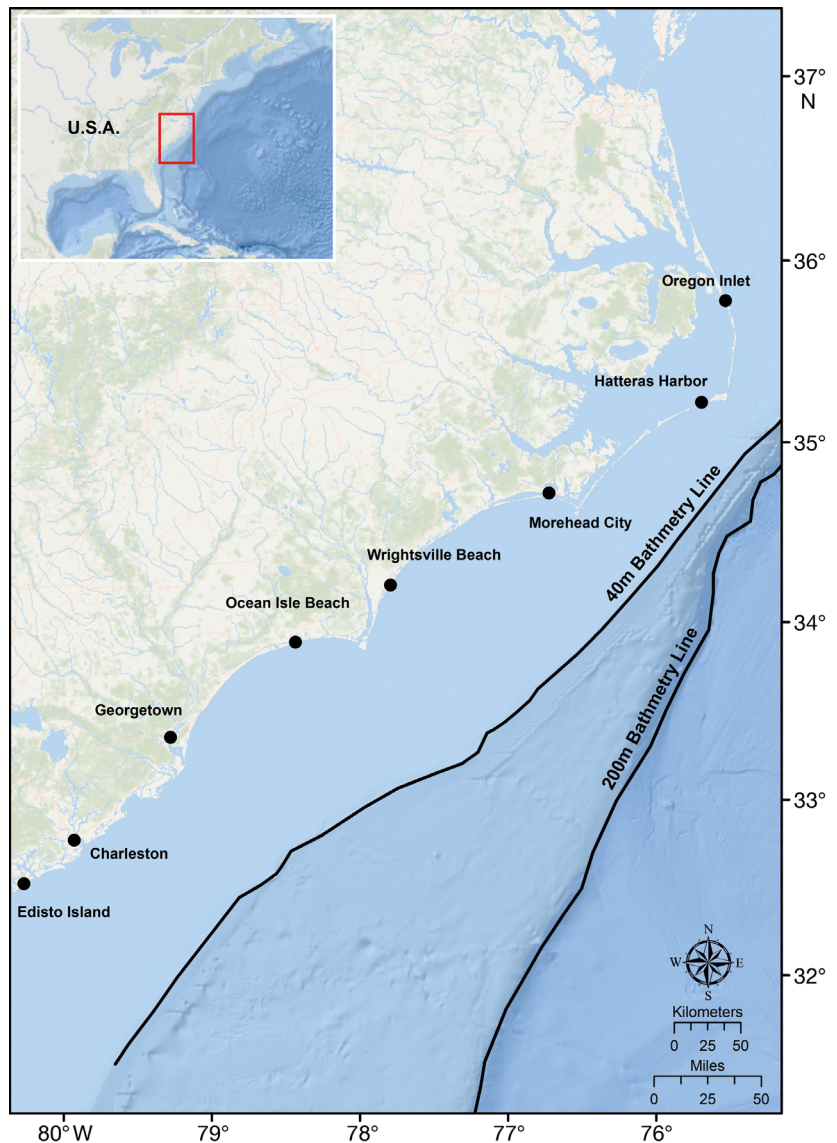

Fig. 1. Study area in the US South Atlantic with a focus on the upper South Carolina and North Carolina coasts. The locations of all ports where fish were sampled are indicated (•)

2.2. Stomach content analysis

In the laboratory, stomachs were thawed and prey items were removed and rinsed with deionized water. Prey items were identified to the lowest taxonomic level (typically genus and species) based on external morphology and comparisons with published references (e.g. Gosner 1971, Carpenter 2002), enumerated, blotted dry, and weighed wet to the nearest gram. Whole prey sizes were measured (in millimeters) for teleosts (TL: total length), crustaceans (CL: carapace length), or cephalopods (ML: mantle length).

Digestion state was categorized for each stomach item using a 0 to 4 scale (0, indigestible, e.g. parasites, plastic trash, terminal tackle, *Sargassum* algae; 1, no evidence of digestion; 2, <50% digested; 3, >50% digested; 4, only hard structures remained). Partially digested prey, cephalopod beaks, fish bones, and otoliths recovered from stomachs were identified using taxon-specific keys (Clarke 1986, Campana 2004) as well as specimen reference collections. For these prey items, original body size was reconstructed using published equations or equations generated from whole prey items recovered during this study. Either lower rostral length or lower hood length was used for squid and octopods, respectively; whereas caudal peduncle depth, eye diameter, and/ or otolith diameter were used to reconstruct fish prey sizes (Staudinger et al. 2009, 2013, Xavier & Cherel 2009). Stomachs containing only recently consumed bait were categorized as empty, and empty stomachs were enumerated for each predator.

Diet was characterized separately for each predator species using gravimetric, numeric, and frequency of occurrence indices of recovered prey. For unique prey types, mean percent abundance ($\overline{\%N}$), mean percent mass ($\overline{\%M}$), and the percent frequency of occurrence (%FO) were each calculated. The proportional composition by abundance and weight of each prey type was calculated separately for each predator stomach and then averaged over all non-empty stomachs for each predator species, following:

$$\overline{\%N} = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{N_{ij}}{\Sigma_{i=1}^{Q}N_{ij}}\right)\times 100 \qquad (1)$$

where P is the number of fish recovered with non-empty stomachs, Q is the number of prey types in all of the samples, and N_{ij} is the number of prey type i in predator j. Mean percent mass was calculated as:

$$\overline{\%M} = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{W_{ij}}{\Sigma_{i=1}^{Q}W_{ij}}\right)\times 100 \qquad (2)$$

where P and Q are defined as in Eq. (1) and W_{ij} is the mass of prey type i in predator j.

Percent frequency of occurrence (%FO) was calculated as:

$$\%FO = \frac{J_i}{P_J}\times 100 \qquad (3)$$

where J_i is the number of individuals of predator J containing prey type i and P_J is the number of predator J recovered with identifiable prey in the stomach. As calcified structures can accumulate in predator stomachs over multiple feeding events, resulting in a positive bias in the representation of those prey species in the diet, stomachs that contained only prey items categorized with a digestive state of '4' were excluded from $\overline{\%N}$ and $\overline{\%M}$ estimates (Chipps & Garvey 2007). However, these stomachs were included in the estimation of %FO because the index is based only on the presence or absence of a prey and is not severely biased by prey digestion times.

Species accumulation curves were used to determine if sampling effort (number of stomachs examined) for each predator species was sufficient to describe their overall dietary niche breadth. The stomach contents of individual predators were organized by major prey families and characterized as present or absent. Species accumulation curves were generated using the specaccum function in the vegan package in R (R Core Team 2017). The 'random' method with 100 permutations and sampling without replacement was used to find the mean (±SD) species accumulation curve for each predator. A plateau in prey richness is indicated when the curve reaches an asymptote at an *x*-axis value ≤ the sample size of the predator species, meaning that examination of additional stomachs is unlikely to result in the identification of novel prey items (Cook & Bundy 2010). The minimum derivative (md) of the curve was calculated to determine if an asymptote was reached using a cutoff value of 0.05.

2.3. Predator–prey body size relationships

The allometry of size-based feeding habits for each of the 4 predator species was evaluated using quantile regression models (Scharf et al. 1998, Cade et al. 1999, Scharf et al. 2000). Bivariate scatter plots were generated from measured or estimated body lengths of prey (dependent variable) and predators (independent variable). Upper (90th or 95th quantiles) and lower (5th or 10th quantiles) bounds, as well as median prey sizes (50th quantiles), were used to explore ontogenetic changes in predator–prey size relationships. Choice of quantiles was determined based on sample size (Scharf et al. 1998). Relative prey sizes eaten (prey length/predator length) were calculated and evaluated as a function of predator body size to quantify ontogenetic changes in trophic niche breadth (e.g. Scharf et al. 2000, Staudinger & Juanes 2010, Teffer et al. 2015). Quantile regression models were fit using Stata statistical software (StataCorp), version 10. The cumulative frequency distributions of relative prey sizes eaten were also compared among predator species to assess the degree of niche overlap.

2.4. Dietary overlap

Schoener's index (Schoener 1970) was used to estimate the degree of diet overlap among predators overall and separately during spring, summer, and fall seasons based on the average percent mass of prey types represented in the diets. Schoener's index was calculated as:

$$\alpha = 1.0 - 0.5 \times \sum_{i=1}^{n} |p_{ij} - p_{ik}| \qquad (4)$$

where j and k represent the 2 predator species being compared, p_{ij} is the contribution of prey type i to the total mass of all prey eaten by predator j, and p_{ik} is the contribution of prey type i to the total mass of all prey eaten by predator k, and n is the total number of prey types eaten by one or both predators. Values for α range from 0 (no overlap) to 1 (complete overlap) and values of 0.6 or greater are generally considered to represent ecologically significant overlap (Schoener 1970).

2.5. Multivariate analysis

We applied both analysis of similarity (ANOSIM) and non-metric multidimensional scaling (NMDS) to predator diet data to identify factors contributing to variation in food habits and to ordinate complex trophic patterns in simple 2- or 3-dimensional space. For these analyses, prey were grouped into guilds based on taxonomic relatedness, similarities in body size, and/or habitat associations. This resulted in 8 prey guilds, which included (1) decapod crustaceans, (2) small, non-decapod crustaceans, (3) sargassum-associated prey (Monacanthidae, Diodontidae, Balistidae, Tetraodontidae, small Carangidae, juvenile Coryphaena, and Portunid crabs), (4) Family Exocoetidae (flying fishes), (5) large Carangidae (smaller Carangidae were included in the sargassum-associ-

ated prey guild), (6) Family Scombridae (mackerels), (7) Family Argonautidae (paper nautilus), and (8) Order Teuthida (squids). The percent by mass $\overline{\%M}$ of each prey guild was calculated for each predator stomach and used as the dietary metric for ordination analyses to broadly reflect the importance of common prey guilds within this pelagic food web. Explanatory factors included predator species, sex, and body size, as well as season, year, and latitude. For multivariate analyses, predator body sizes were categorized into seven 25 cm size bins. Seasons were defined as spring (March to May), summer (June to August), fall (September to November), and winter (December to February). Latitude included 3 categories, for fish caught below 33° N, between 33° and 35° N, and above 35° N, based on aspects of the bathymetry that varied regionally and the location of primary fishing ports. For each of the 4 predator species, we first explored the trophic patterns using ANOSIM to identify dissimilarities in food habits due to sex or body size, and also season, year, and latitude. We then conducted NMDS ordination on the full data set (all predator species) to visualize the trophic relationships in a reduced number of dimensions (2 or 3), followed again by ANOSIM to examine sources of dissimilarity among predators. For NMDS, we report both 2- and 3-dimensional stress scores. For ANOSIM, we report R statistics (and associated p-values) calculated from rank dissimilarities. Multivariate analyses were conducted using PRIMER software version 7.0.

3. RESULTS

3.1. Stomach content analysis

Stomach contents were analyzed for a total of 1226 individual predators (Table 1). The proportion of stomachs containing prey was high (85.3%) and a broad

Table 1. Number of stomachs and fish body sizes (curved fork length) sampled for diet analysis of blackfin tuna, dolphinfish, wahoo, and yellowfin tuna during April 2010 to October 2013. Seasons defined by months (see Section 2.5). n: total number of fish collected; with prey: fraction of stomachs containing prey

Species	n	With prey (%)	n per season				Size (cm)	
			Winter	Spring	Summer	Fall	Mean ± SD	Range
Blackfin tuna	285	(93.7)	37	97	53	98	65.1 ± 11.6	28.5–94.5
Dolphinfish	457	(83.2)	0	195	249	13	86.6 ± 21.3	35.6–140.4
Wahoo	239	(60.3)	1	45	107	86	130.6 ± 16.5	91.0–177.0
Yellowfin tuna	245	(77.1)	0	55	182	8	94.7 ± 13.8	46.6–140.7
Total stomachs	1226	(85.3)						

range of body sizes was examined across predator taxa. The temporal resolution and extent of our sampling approach provided trophic information for at least 2 seasonal periods for each species, with information during 3 and 4 seasonal periods for wahoo and blackfin tuna, respectively. Collectively, the 4 predator species consumed a diverse assemblage of prey, which included 123 different prey taxa representing 66 orders and/or families (Table 2, Table S1

in the Supplement at www.int-res.com/articles/suppl/m631p181_supp.pdf). Fish prey occurred most consistently across predator diets, being recovered from 73 to 95% of stomachs that contained food, depending on predator species. In terms of prey mass, fish prey dominated the diets of wahoo ($\overline{\%M}$ = 92.7) and dolphinfish ($\overline{\%M}$ = 81.8), but were much less important to blackfin tuna ($\overline{\%M}$ = 33.9). Crustacean and Molluscan prey contributed more to the

Table 2. Major prey groups (**bold** text indicates group totals) recovered from the stomachs of blackfin tuna, dolphinfish, wahoo, and yellowfin tuna in US South Atlantic waters. Prey groups included in this table contributed ≥1% by mass ($\overline{\%M}$) or occurred in ≥1% of predator stomachs (%FO) for at least 1 of the 4 predator species; empty cells indicate the absence of a prey taxon from the predator diet. Taxonomic classifications are limited to Family for brevity. Reported totals are cumulative (rounded to 1 decimal place) and include diet items that were identified to a lower level as well as items that could only be identified to a broader taxonomic classification. A comprehensive diet table is included as Table S1 in the Supplement. UID: unidentified

Prey taxon	Blackfin tuna			Dolphinfish			Wahoo			Yellowfin tuna		
	%FO	$\overline{\%M}$	$\overline{\%N}$	%FO	$\overline{\%M}$	$\overline{\%N}$	%FO	$\overline{\%M}$	$\overline{\%N}$	%FO	$\overline{\%M}$	$\overline{\%N}$
Crustacean prey	**73.4**	**46.4**	**42.9**	**24.5**	**10.6**	**11.8**	**1.4**	**<0.1**	**0.4**	**43.9**	**21.7**	**26.3**
Amphipoda	15.4	4.4	3.9							43.2	10.6	9.7
Decapoda	46.4	21.6	20.4	21.8	9.9	10.3	0.7	<0.1	0.2	28.6	8.5	11.7
Aristeidae	1.9	0.3	0.3	0.3	<0.1	0.1				5.3	1.8	1.7
Portunidae	2.6	0.9	0.9	16.8	8.3	7.6				5.8	0.5	1.4
Sicyoniidae	1.1	0.3	0.4	1.3	0.2	0.4						
Isopoda	15.7	4.6	3.9	0.3	0.3	0.2				0.5	0.2	0.2
Stomatopoda	27.3	9.5	9.4	0.5	0.1	0.2				2.1	0.7	0.9
UID crustaceans	21.3	5.8	4.9	2.6	0.3	1.1	0.7	<0.1	0.2	5.3	1.8	3.8
Fish prey	**73.8**	**33.9**	**32.0**	**89.7**	**81.8**	**77.0**	**95.1**	**92.7**	**83.5**	**78.3**	**62.2**	**53.5**
Exocoetidae	11.6	8.0	7.6	22.9	19.2	12.8	4.2	3.0	2.6	3.7	3.3	2.6
Clupeidae	1.8	0.5	0.5				0.7	0.1	0.2			
Dussumieriidae	1.1	0.5	0.5	2.4	1.7	1.7	0.7	0.7	0.3	1.6	1.4	0.8
Myctophidae	1.1	0.2	0.2	0.3	0.1	0.1	0.7	<0.1	0.2			
Bramidae	0.7	0.2	0.4	0.3	<0.1	<0.1	0.7	0.7	0.6	1.6	0.7	0.7
Carangidae	3.7	1.2	1.1	16.8	9.0	8.1	3.5	1.8	1.6	4.8	3.6	2.8
Coryphaenidae				2.9	1.7	1.8						
Echeneidae	1.5	0.6	0.6				0.7	0.6	0.3	0.5	0.1	0.3
Scombridae	6.4	3.4	3.1	4.2	3.3	2.4	43.7	41.7	28.7	20.6	20.0	14.9
Serranidae	1.1	0.2	0.2	1.1	0.4	0.3	1.4	0.5	0.5	1.6	0.7	0.8
Stromateidae	5.3	1.9	1.8	3.4	1.5	1.7	0.7	0.7	0.6	1.6	0.2	0.4
Trichiuridae	1.1	0.2	0.3	1.1	0.3	0.3	0.7	<0.1	0.2	1.6	0.8	0.5
Syngnathidae	3.7	0.6	0.7	1.6	0.6	0.8				2.1	0.4	0.6
Balistidae	0.7	0.1	0.1	3.7	1.4	1.3	1.4	0.9	0.7	1.1	0.3	0.3
Diodontidae				10.3	4.5	4.5	4.2	2.1	2.6	1.6	0.3	0.4
Monacanthidae	4.9	1.1	1.0	20.0	8.8	8.5	2.8	1.8	1.4	6.9	2.6	2.1
Tetraodontidae	2.6	0.5	0.5	2.6	1.3	1.3	2.1	1.8	1.6	3.7	0.9	1.0
UID fish	49.1	13.5	12.4	45.3	25.5	29.1	45.8	34.1	39.9	44.4	25.2	23.8
Molluscan prey	**58.4**	**19.7**	**25.0**	**16.3**	**7.6**	**10.9**	**14.1**	**7.3**	**16.1**	**33.3**	**15.4**	**19.8**
Cephalopoda	50.2	15.4	20.5	14.2	7.0	9.9	14.1	7.3	16.1	32.3	15.2	19.2
Octopoda	12.0	2.2	3.0	5.8	2.4	3.4	4.2	2.8	3.5	4.2	2.0	4.3
Argonautidae	8.2	1.7	2.1	5.0	2.2	3.1	4.2	2.2	3.1	3.2	1.4	3.2
Teuthida	43.8	11.7	15.9	7.9	4.1	5.7	11.3	4.1	11.8	27.5	13.1	14.6
Enoploteuthidae	0.7	0.1	0.1							1.6	0.2	0.5
Loliginidae	4.9	1.2	1.4	0.5	0.5	0.4	2.8	0.4	1.5			
Ommastrephidae	16.9	5.3	5.7	4.2	2.7	2.8	5.6	2.2	3.3	19.6	9.8	7.8
Onychoteuthidae	2.2	0.4	0.4	0.3	<0.1	0.1						
Gastropoda	13.5	4.2	4.4	2.1	0.6	1.0				1.6	0.2	0.6
Cavoliniidae	6.7	2.1	2.3	0.8	<0.1	0.3						
Atlantidae	3.0	0.7	0.7	0.5	0.3	0.4				0.5	<0.1	0.2

diets of blackfin and yellowfin tuna (crustaceans: %FO = 44–73, $\overline{\%M}$ = 22–46; molluscs: %FO = 33–58, $\overline{\%M}$ = 15–20), relative to wahoo and dolphinfish. In fact, crustacean prey, particularly decapods, contributed most of the prey mass ($\overline{\%M}$ = 46.4) to blackfin tuna diets. Squids and pelagic octopods *Argonauta* spp. were the most commonly recovered Molluscan prey, although blackfin tuna diets also routinely included Gastropods. Species accumulation curves reached an asymptote (md < 0.05) for all 4 predator species, indicating that sampling effort was adequate to assess dietary diversity (Fig. 2).

Blackfin tuna displayed a high level of diversity in their feeding habits, with 46 unique prey families represented (Tables 2 & S1). A unique feature of blackfin tuna feeding ecology was that although crustaceans, fishes, and molluscs were each represented in their diets, they were the only predator for which fish prey did not comprise the majority of the diet by mass (Fig. 3). Crustaceans representing several taxonomic orders (Amphipoda, Decapoda, Isopoda, and Stomatopoda) combined to account for almost half of the prey mass consumed by blackfin tuna, with stomatopods occurring in more than a quarter of blackfin tuna stomachs. The fish prey consumed by blackfin tuna were also diverse, with needlefish (Belonidae), flying fishes (Exocoetidae), and small scombrids (Scombridae) contributing most to patterns of prey occurrence and prey mass.

Ommastrephid squids and pelagic octopods *Argonauta* spp. were much more common in blackfin tuna diets than any of the other predator species, with squids accounting for nearly 12% of the prey mass eaten, nearly 3-fold greater than the contribution of squids to the diets of dolphinfish and wahoo.

Similar to blackfin tuna, the feeding habits of yellowfin tuna revealed a consistent reliance on invertebrate prey (crustaceans and molluscs). While only moderately diverse in terms of the number of unique prey taxa recovered from the stomachs (37 prey families), yellowfin tuna frequently included amphipods, decapods, and cephalopods in their diets (Tables 2 & S1; Fig. 3). Still, fish prey were the most important prey type overall. Scombrids, primarily *Auxis* spp., were of primary importance (%FO = 20.6; $\overline{\%M}$ = 20.0), while flying fish (Exocoetidae), jacks (Carangidae), needlefish (Belonidae), and filefish (Monacanthidae) occurred with moderate regularity (%FO = 3–7). Yellowfin tuna diets were second only to blackfin tuna in the frequency of occurrence and contribution by mass (%FO = 32.3; $\overline{\%M}$ = 15.2) of cephalopod prey, which consisted primarily of ommastrephid squids.

Dolphinfish demonstrated the most diverse feeding habits of the 4 predators, with 48 unique prey families recovered from their stomachs (Tables 2 & S1). Many of the prey species found to be important to dolphinfish diets are typically associated with *Sargassum* algae and other floating debris in the pelagic environment, including needlefish (Belonidae), flying fish (Exocoetidae), jacks (Carangidae), filefish (Monacanthidae), porcupinefish (Diodontidae), triggerfish (Balistidae), pufferfish (Tetraodontidae), smaller conspecifics, and swimming crabs within the family Portunidae (Tables 2 & S1, Fig. 3). Indeed, *Sargassum* algae was recovered from nearly one-third of all dolphinfish stomachs (%FO = 29.1), although it was likely consumed incidentally during prey capture. Other than *Sargassum*-associated prey, flying fish were the most important dietary item for dolphinfish predators, occurring in 23% of stomachs and accounting for nearly 20% of the diet by mass. Dolphinfish also relied on cephalopod prey to a moderate extent (%FO = 14.2), but much less so than blackfin tuna.
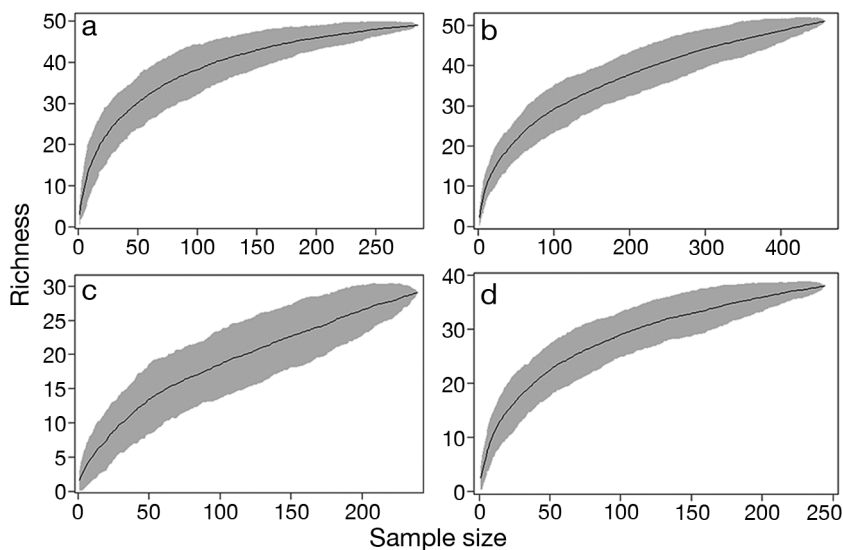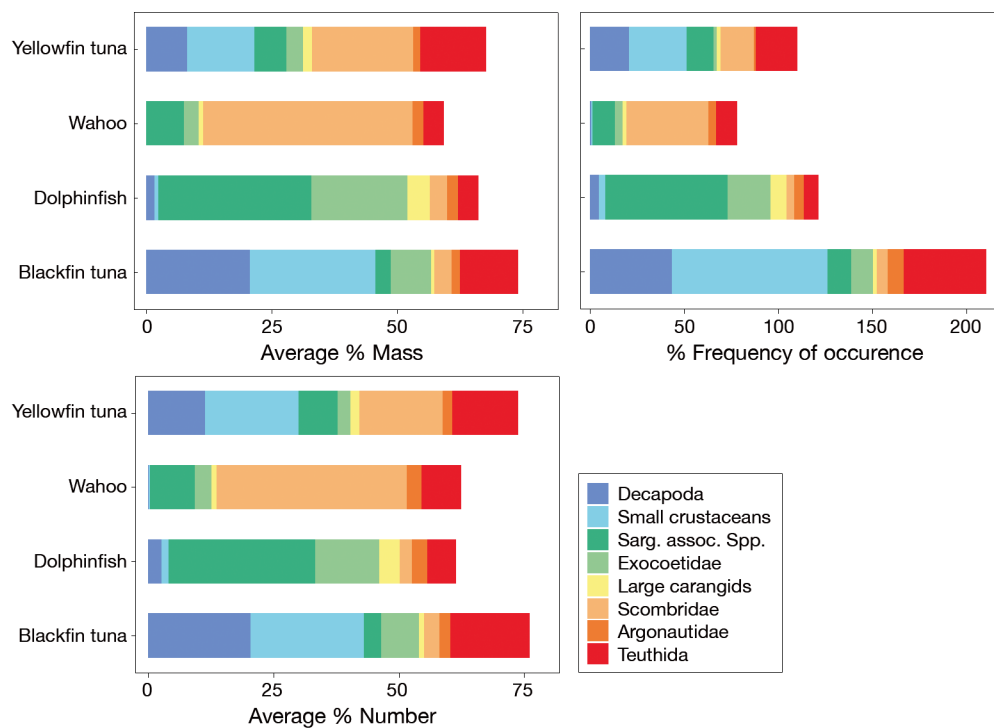

Fig. 2. Species accumulation curves and 95% confidence intervals for (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna. Sample size and minimum derivative (md) values for each predator were: blackfin tuna (n = 285; md = 0.02), dolphinfish (n = 457; md = 0.02), wahoo (n = 239; md = 0.04), and yellowfin tuna (n = 245; md = 0.03). Richness: number of unique prey families recovered from predator stomachs; sample size: number of stomachs examined for each predator species

Fig. 3. Dietary indices of the pelagic predator species blackfin tuna, dolphinfish, wahoo, and yellowfin tuna in US South Atlantic waters calculated for the 8 major prey guilds (described in Section 2.5) and included in the NMDS analyses

Wahoo were chiefly piscivorous (fish prey: 95% FO and 93% by mass, overall) and displayed the least diverse feeding habits among the predator species examined, including only 27 unique prey families in their diet (Tables 2 & S1, Fig. 3). Scombrids (mainly *Auxis* spp.) were the dominant prey (%FO = 43.7; $\overline{\%M}$ = 41.7), with flying fish (Exocoetidae), needlefish (Belonidae), jacks (Carangidae), and pufferfish (Diodontidae) contributing to a lesser degree (up to 4.2%FO). Wahoo consumed only trace amounts of crustacean prey and moderate amounts of cephalopods (%FO = 14.1; $\overline{\%M}$ = 7.3).

3.2. Predator–prey body size relationships

Of the 4 predators, wahoo were the largest on average (130.6 cm CFL), followed by yellowfin tuna (94.7 cm CFL), and dolphinfish (86.6 cm CFL). Blackfin tuna was the smallest predator overall (65.1 cm CFL), less than half the mean size of wahoo (Table 1). As expected given the differences in body size, wahoo consumed the largest prey sizes (mean fish prey size = 20 cm TL). Median prey sizes eaten by wahoo closely tracked the ontogenetic changes in maximum prey sizes eaten (Fig. 4). In contrast, blackfin tuna and dolphinfish consumed considerable

amounts of small-bodied prey (<5 cm), and median prey sizes were nearly flat across the range of predator body size sampled. However, dolphinfish did consume larger cephalopod prey (mean size = 12.3 cm ML) than other predators (Table 3). With the exception of yellowfin tuna, predators displayed ontogenetic increases in maximum prey sizes consumed, while maintaining similar minimum prey sizes in the diet, even at the largest predator body sizes resulting in a classic wedge-shape to the overall distribution of prey sizes in their diets (Table 3, Fig. 4). Fish prey generally represented the largest prey (mean size ≈ 8–20 cm TL) consumed by all predators, with the exception of small (<65 cm CFL) blackfin tuna, for which cephalopods were the largest prey eaten. Crustaceans (mean size ≈1–3 cm CL) and gastropods represented the smallest prey consumed across the range of predator body sizes, while the cephalopods eaten were consistently between 5 and 20 cm ML (mean ML ≈ 6–12 cm). As such, fish prey demonstrated the most dynamic range in body sizes of all prey consumed. With the exception of wahoo, median prey sizes increased only marginally at larger predator body sizes, and were constrained by the considerable number of smaller prey body sizes consumed (Fig. 4).

Ontogenetic patterns in relative prey sizes consumed indicated increasing trophic niche breadths

Table 3. Results from quantile regression models fit to predator–prey body size relationships (minimum prey size: 5th/10th quantile; median prey size: 50th quantile; maximum prey size: 90th/95th quantile). Parameter estimates (β_0 and β_1) are presented with bootstrapped estimates of standard error (SE). p: the significance level for the regression coefficient (β_1); Fish, Crust, and Ceph: mean prey size for fish prey (total length, TL), crustacean prey (carapace length, CL), and cephalopod prey (mantle length, ML), respectively, for each predator species. Results from models estimating relative prey sizes eaten as a function of predator body size are presented in Table S2 in the Supplement

Predator species	Quantile	β_0 (SE)	β_1 (SE)	p	Mean prey size (cm) Fish	Crust	Ceph
Blackfin tuna					11.1	1.7	5.9
(n = 742)	5th	−1.78 (0.57)	0.04 (0.01)	<0.01			
	50th	−6.18 (0.60)	0.14 (0.01)	<0.01			
	95th	−18.51 (2.95)	0.55 (0.04)	<0.01			
Dolphinfish					8.1	2.8	12.3
(n = 873)	5th	0.93 (0.38)	0.01 (0.004)	<0.01			
	50th	2.96 (0.81)	0.02 (0.01)	0.06			
	95th	−11.33 (2.34)	0.39 (0.04)	<0.01			
Wahoo					20.0	NA	11.9
(n = 88)	10th	9.50 (5.14)	−0.05 (0.04)	0.27			
	50th	−16.12 (13.48)	0.24 (0.11)	0.04			
	90th	−48.36 (18.88)	0.60 (0.15)	<0.01			
Yellowfin tuna					13.1	2.9	7.9
(n = 450)	5th	−0.32 (0.46)	0.02 (0.01)	<0.01			
	50th	−2.71 (0.56)	0.08 (0.01)	<0.01			
	95th	13.80 (14.13)	0.16 (0.15)	0.28			

ator body size). Wahoo consumed the largest relative prey sizes on average (mean = 12% of predator body size), with much greater contributions of larger prey (>20% of predator size).

3.3. Multivariate analyses and dietary overlap

Dietary overlap among predator species was low (≥0.40) for three of the pairwise comparisons, but Schoener's index values indicated ecologically significant overlap between yellowfin tuna and wahoo (0.77), blackfin tuna and dolphinfish (0.65), and moderate dietary overlap (0.50) between blackfin and yellowfin tuna (Table 4). Dietary overlap during spring (0.60) was the primary season driving overlap values for blackfin tuna and dolphinfish due to large contributions of flying fish (Exocoetidae) and, to a lesser extent, argonauts and filefish (Monocanthidae). Out-

for larger predators, with the exception of yellowfin tuna, which did not demonstrate appreciable changes in relative prey size with growth (Fig. 5, Table S2 in the Supplement). Similar to ontogenetic patterns observed for absolute prey sizes eaten, maximum relative prey sizes increased from approximately 0.20 to 0.40 as body size increased for blackfin tuna, dolphinfish, and wahoo. Minimum relative prey sizes eaten remained small (2–3% of predator size; 7–8% for wahoo) and relatively constant across the range of predator body sizes sampled. Quantile regressions for minimum and maximum relative prey size for yellowfin tuna did not produce statistically significant slope coefficients (Table S2), indicating no size-based change in trophic niche breadth. Both tuna species demonstrated a strong dependence on small-bodied prey (<10% of predator size) with skewed relative prey size distributions that included long right-hand tails consisting of low numbers of larger prey (20–40% of predator size) (Fig. 6). Dolphinfish consumed many more prey with relatively larger body sizes (up to 20% of predator size), and also consumed low numbers of much larger prey (20–40% of pred-

Table 4. Schoener's index of dietary overlap among predators calculated using percent mass for prey pooled across all seasons and years (Total), and separately for each season pooled across years. Winter data were not included due to low sample sizes for all predators except blackfin tuna. Index values ≥0.60 were considered to represent significant overlap in diet and are denoted in **bold**

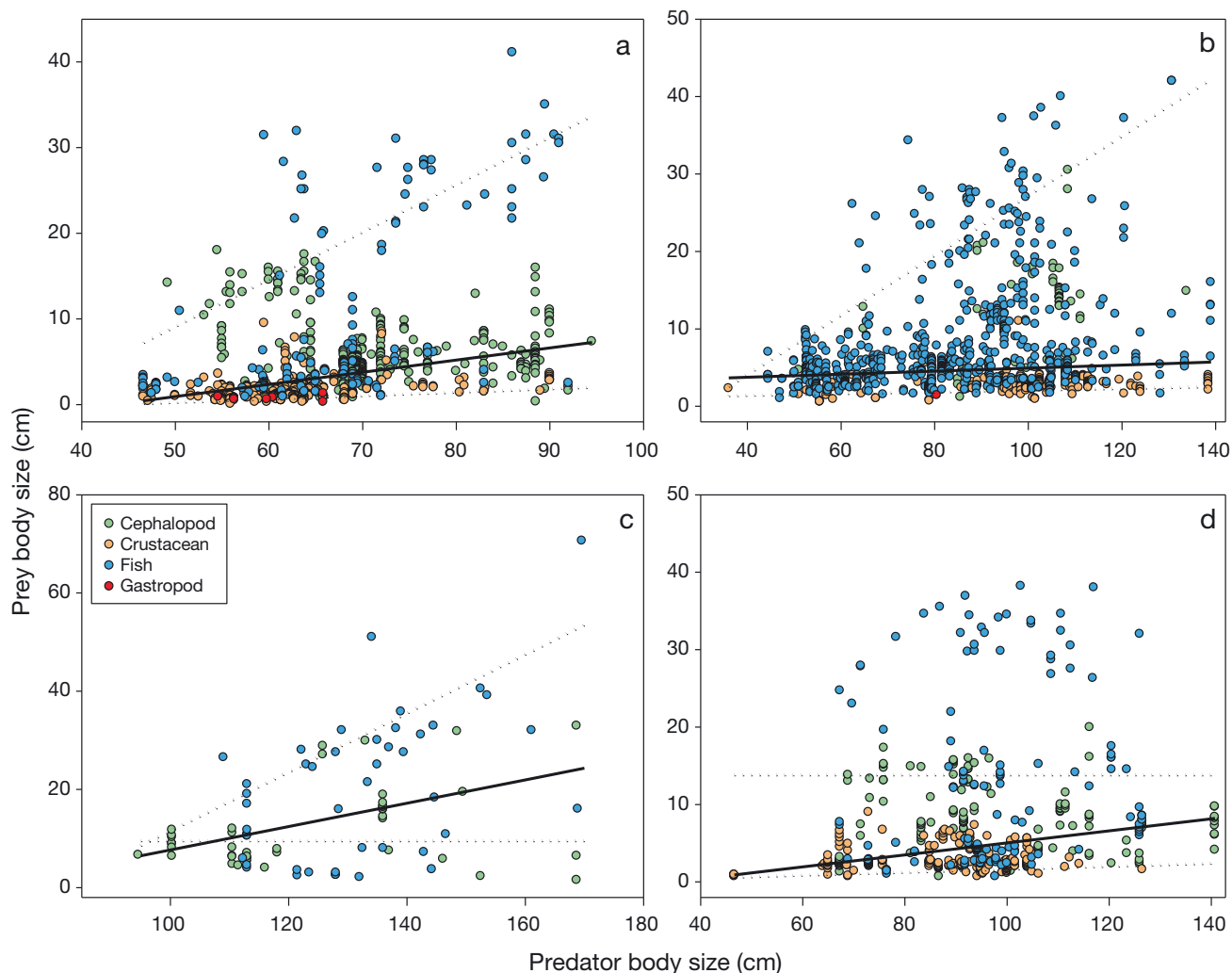| Season and predator	Dolphinfish	Wahoo	Yellowfin tuna
Total			
Blackfin tuna	**0.65**	0.37	0.50
Dolphinfish		0.29	0.37
Wahoo			**0.77**
Spring			
Blackfin tuna	**0.60**	0.01	0.03
Dolphinfish		0.01	0.04
Wahoo			**0.94**
Summer			
Blackfin tuna	0.27	0.34	0.38
Dolphinfish		0.22	0.27
Wahoo			**0.65**
Fall			
Blackfin tuna	0.01	0.50	0.52
Dolphinfish		0.03	0.23
Wahoo			0.39

Fig. 4. Predator–prey body size relationships for (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna in US South Atlantic waters. (Solid line) Median prey size as a function of predator size; (Dotted lines) maximum and minimum prey sizes eaten as a function of predator body size. Regression coefficients are presented in Table 3. Note that axis scaling differs among species plots

side of spring, blackfin tuna diets were more similar to yellowfin tuna, mainly due to their shared reliance on invertebrate prey. Nearly complete overlap in the spring diets of yellowfin tuna and wahoo was estimated (0.95), as well as significant overlap during summer (0.65), due to shared high reliance on scombrid fishes.

When the diets of each predator species were analyzed separately, only blackfin tuna demonstrated significant rank dissimilarities for any of the factors (season, year, latitude, sex, and body size) that we examined. For blackfin tuna, there were significant dissimilarities among seasons (ANOSIM R = 0.168, p < 0.01) and body sizes (ANOSIM R = 0.189, p < 0.01). Blackfin tuna diets differed between fall and winter/spring periods, and also between the largest

body sizes (75–100 cm FL) and smaller individuals (both 25–50 cm and 50–75 cm FL). While NMDS analyses for each predator species revealed low levels of 2-dimensional stress (all 2D stress ≤ 0.10), the other species did not demonstrate significant levels of dissimilarity for the factors that we were able to explore.

When all predator species were analyzed together in a single NMDS analysis, overall 2D stress was low (0.08), indicating good preservation of the original rank dissimilarities (Fig. 7). Predator species was responsible for the majority of the dissimilarity in diet (ANOSIM R = 0.213, p < 0.01), with the greatest dissimilarity occurring between wahoo and blackfin tuna (R = 0.401), wahoo and dolphinfish (R = 0.265), and between blackfin tuna and dolphinfish (R = 0.213). Diets of blackfin and yellowfin tuna were the
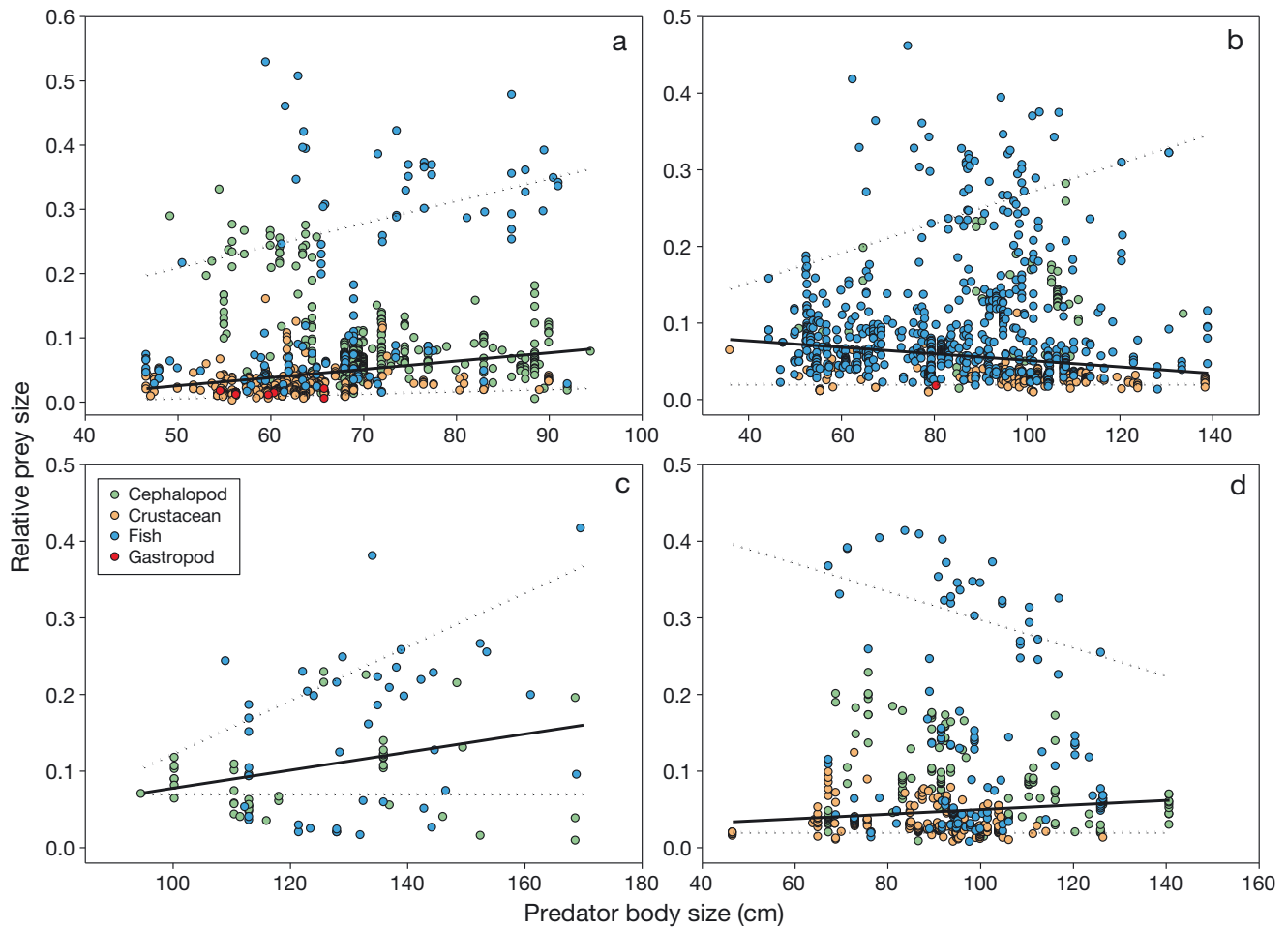
Fig. 5. Relative prey size relationships for (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna in US South Atlantic waters. (Solid line) Median relative prey size as a function of predator size; (Dotted lines) maximum and minimum relative prey sizes eaten as a function of predator body size. Regression coefficients are presented in Table S2. Note that axis scaling differs among species plots

least dissimilar (R = 0.075). While other factors were responsible for significant levels (ANOSIM, p < 0.01) of diet dissimilarity, the magnitude of dissimilarity was much smaller (R scores < 0.10). Differences due to predator body size (R = 0.08) stemmed mainly from diets of the largest predators (>125 cm FL), which set them apart from most other size groups. Seasonal differences (R = 0.04) primarily reflected differences between diets in spring and all other seasons. Latitudinal differences (R = 0.02) occurred between diets of predators caught below 33° N and above 35° N.

The seasonal variation in predator foraging habits was strongest for blackfin tuna, which was detected by the multivariate analysis (ANOSIM). During winter, blackfin tuna relied exclusively on crustacean prey resources, with relatively lower contributions during the warmer seasonal periods (Fig. 8). Fish prey, particularly flying fish, dominated

blackfin tuna feeding habits only during the spring. Dolphinfish also demonstrated an increased reliance on flying fish during spring, yellowfin tuna consumed more fish prey during summer, and wahoo showed a slight increase in cephalopod prey during spring, but the seasonal fluctuations in the diets of these 3 predators were not strong enough to be detected during species-specific multivariate analyses (ANOSIM).

4. DISCUSSION

The simultaneous evaluation of multiple sympatric predators — yellowfin tuna, blackfin tuna, dolphinfish, and wahoo — revealed clear differences in overall, seasonal, and size-based dietary niches within the pelagic ecosystem of the South Atlantic Bight. Dietary indices of overlap and multivariate NMDS
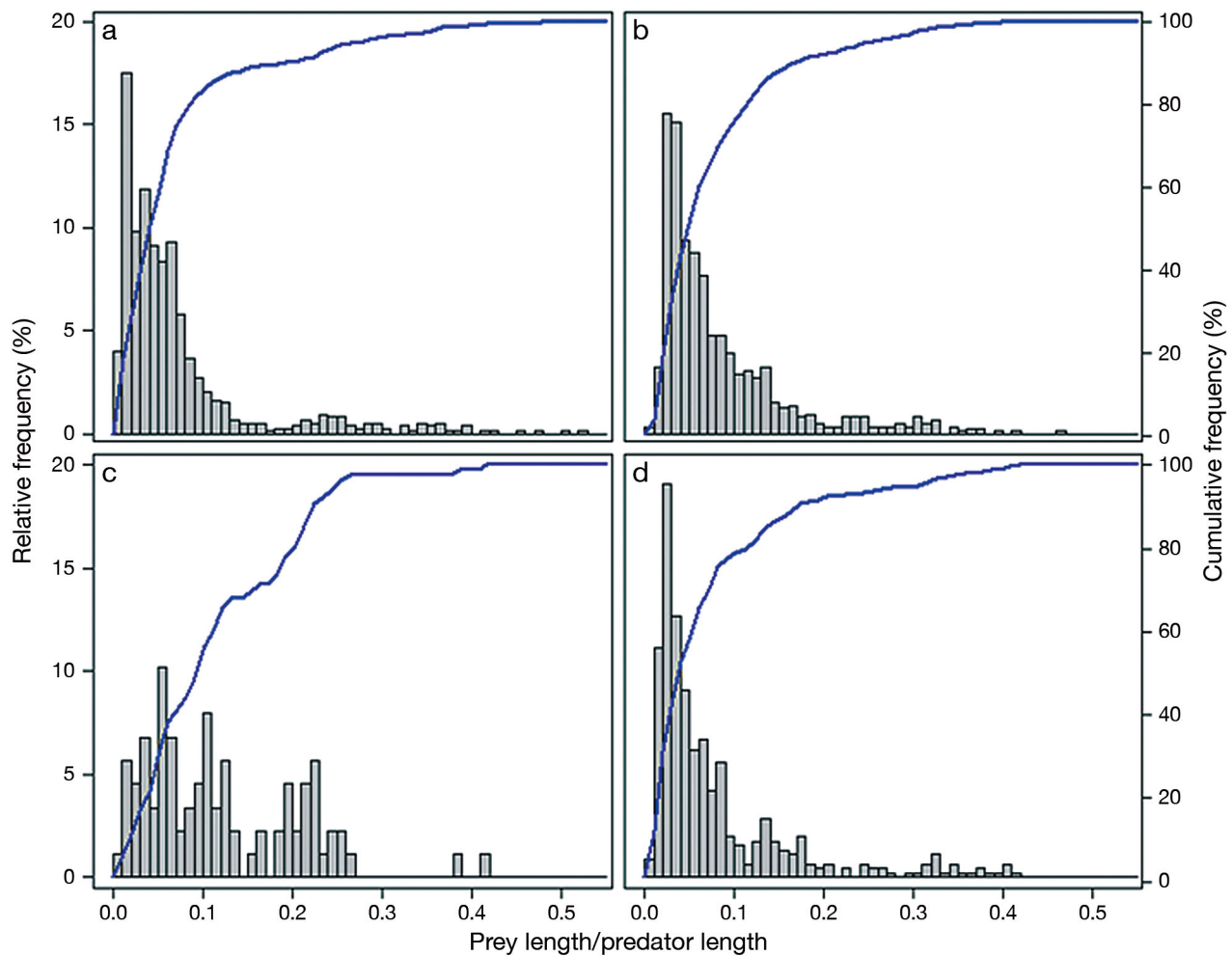
Fig. 6. Relative (histograms) and cumulative (line plots) frequencies of prey–predator body size ratios (relative prey sizes) consumed by (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna in US South Atlantic waters
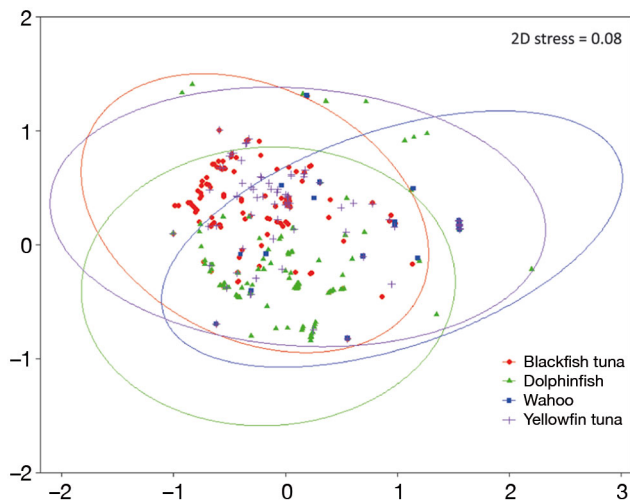

Fig. 7. NMDS ordination scores for each of the 4 pelagic predator species blackfin tuna, dolphinfish, wahoo, and yellowfin tuna in US South Atlantic waters. The 95% confidence ellipses are shown for each predator species

analyses were aligned in showing that diet dissimilarities were driven largely by predator species and that spring was a unique season for the foraging ecology of the guild, and ecologically significant overlap was observed between some predators. Seasonal shifts in predator diets were evident for all predators; however, sampling effort was fisheries-dependent and may have influenced these patterns. Most diet data were collected during the summer for tunas and dolphinfish, and higher numbers of wahoo were sampled during spring and fall. The greatest differences among species overall were found between wahoo and blackfin tuna, the largest and smallest predators on average, primarily due to their respective reliance on fish and crustacean prey. The high diversity of prey families represented in the 4 predator diets suggests they are opportunistic generalists within the pelagic environment of the US South Atlantic, which aligns with the findings from studies of similar spe-
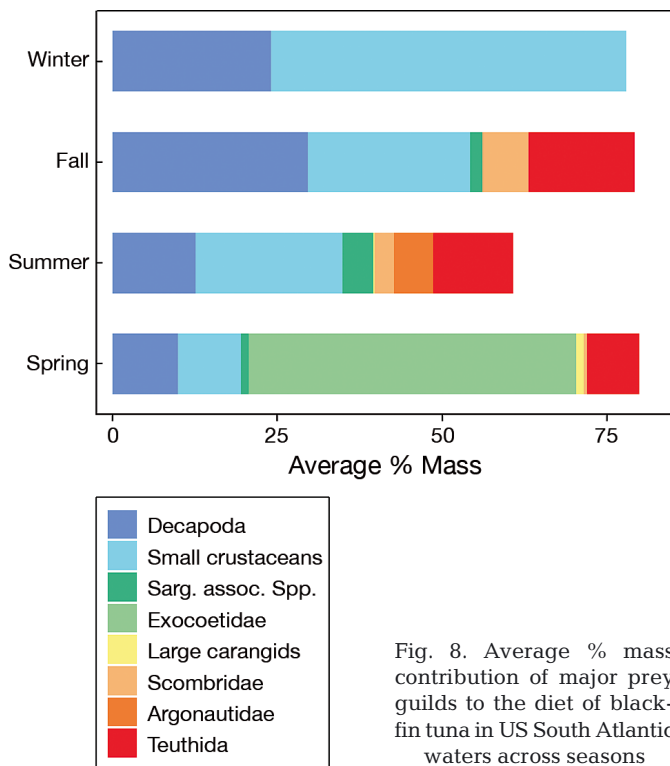
4.1. Species-specific diets

Aspects of the biology and trophic ecology of blackfin tuna, the smallest species of true tuna within the genus *Thunnus*, are known from only a few studies conducted in this region more than 3 decades ago (Collette & Nauen 1983, Manooch & Mason 1983) as well as from the Caribbean (Doray et al. 2004, Headley et al. 2009) and Gulf of Mexico (Cornic & Rooker 2018). The present study represents the most quantitative description of blackfin tuna diets in the US South Atlantic region to date and suggests they have a distinct trophic niche that differs from yellowfin and larger tunas that occupy the NWA. Blackfin tuna primarily consumed an invertebrate-based diet consisting of crustaceans and cephalopods. This differs from observations in the Caribbean where fish were the most important prey item (Headley et al. 2009). Importantly, blackfin tuna were the only predator species in this study for which diet was assessed during the winter season; during this period, blackfin were focused almost exclusively on crustacean prey resources. In contrast, *Sargassum*-associated species, particularly Monacanthid fishes and small Carangids, were more frequent in blackfin tuna diets during summer. It is possible that blackfin tuna alter their foraging behavior and seek refuge in *Sargassum* habitats during summer to avoid seasonally abundant predators such as blue marlin *Makaira nigricans* (Rudershausen et al. 2010, Veiga et al. 2011). The prevalence of crustaceans in their diets year-round suggests blackfin tuna take advantage of seasonal blooms in secondary consumers using ram feeding behavior, which increases the importance of gill rakers as a morphological structure for retention of these small prey items (Magnuson & Heitz 1971). Blackfin supplement their diets with larger fishes and muscular squids either opportunistically in the epipelagic zone or by hunting in mesopelagic waters (Headley et al. 2009). Satellite tagging has revealed blackfin tuna diving to depths up to 220 m, although they spend the vast majority (90%) of their time within the epipelagic zone at depths <57 m (Fenton et al. 2015). Within the US South Atlantic, blackfin tuna appear to undergo an ontogenetic diet shift towards larger prey fishes (≥15 cm) at fork lengths above approximately 65 cm, which aligns with observed shifts documented in other systems (e.g. Headley et al. 2009). Additional electronic tagging studies of blackfin tuna would be useful to understand diurnal and seasonal diving behavior as well as ontogenetic shifts in habitat use within the US South Atlantic Bight ecosystem.

Fig. 8. Average % mass contribution of major prey guilds to the diet of blackfin tuna in US South Atlantic waters across seasons

cies in other regions (Young et al. 2010, Olson et al. 2016, Perelman et al. 2017, Varela et al. 2017). Nonetheless, a few prey groups were disproportionally represented across all 4 predator diets, and their relative availability in the environment is likely an important indicator of predator distribution and growth. Prey common to all predators included small scombrids, needlefish, flying fish, jacks, filefish, argonauts, and ommastrephid squids, and are typical of regional *Sargassum*-associated, epipelagic, and mesopelagic habitats (Casazza & Ross 2008, Rudershausen et al. 2010). In addition, small schooling amphipod and stomatopod crustaceans, as well as decapod crabs, were key invertebrate prey resources for tunas, which is similar to observations for small tunas in other regions, such as albacore *Thunnus alalunga* in northern Atlantic waters (Teffer et al. 2015), and yellowfin tuna on a global scale (Duffy et al. 2017). Collectively, our findings provide a comprehensive assessment of interspecific, seasonal, and size-based foraging patterns for the region, which has been limited to date due to the absence of routine fishery-independent offshore surveys. This information can be used to fill known information gaps needed for ecological assessments (ICCAT 2016), and to support ecosystem-based management efforts in the region.

Yellowfin tuna diets were relatively similar to blackfin tuna with a high occurrence of crustaceans and cephalopods, but included greater contributions of fish prey, particularly small scombrids (*Auxis* spp.) during spring, which led to a nearly complete overlap in diet with wahoo during this season. Aspects of the food habits of yellowfin tuna in the US South Atlantic, particularly the importance of *Auxis* spp. as a prey resource, were similar to observations in the eastern (Varela et al. 2017) and western (Allain 2005) Pacific as well as the western Indian ocean (Potier et al. 2007), while the importance of scombrid fishes (likely *Auxis* spp.) to yellowfin tuna diets has also been noted in global analyses (Duffy et al. 2017). Interestingly, amphipods were the dominant crustacean prey in yellowfin tuna diets across all body sizes, suggesting they take advantage of large aggregations of crustacean prey similar to blackfin tuna. Cephalopod prey recovered from yellowfin tuna stomachs were mostly characterized as fully (with only hard parts remaining) or partially digested. Since fish were landed during the daytime, these results are either indicative of nocturnal foraging on cephalopods or, similar to observations for marine mammal predators (Staudinger et al. 2014), cephalopod beaks accumulating over extended periods of time. As yellowfin tuna grow and become more endothermic, they have been observed to undergo ontogenetic shifts in habitat and diet by expanding their depth range and foraging less on epipelagic prey (Carey & Olson 1982, Vaske et al. 2003, Graham et al. 2007, Schaefer et al. 2007, Weng et al. 2009). Ontogenetic shifts in yellowfin tuna were not detected in the present study, likely because the majority of fish sampled had already attained body sizes larger than the threshold (45–50 cm FL) at which dietary shifts are thought to occur (Graham et al. 2007), and large fish prey were already part of their diets.

Dolphinfish had the most diverse diet of the 4 predators examined but were still mainly piscivorous (%FO and $\overline{\%M}$ > 80%). Compared to other regions in the Atlantic (Logan et al. 2013, Teffer et al. 2015), dolphinfish in US South Atlantic waters consumed more fish and crustacean prey, but less cephalopods. Most prey fish were either *Sargassum*-associated (Monacanthids, Diodontids, or small Carangids) or small schooling species typical of surface waters near the Gulf Stream Current. *Sargassum* algae is an ephemeral habitat, which occurs as floating mats that peak in occurrence during summer and early fall (Coston-Clements & Center 1991, Rooker et al. 2006). While our findings support the role of *Sargassum* as a critical structural foraging habitat throughout the range of dolphinfish which attracts a species-rich as-

semblage of juvenile fishes and crustaceans (Rose & Hassler 1974, Manooch et al. 1984, Coston-Clements & Center 1991, Oxenford & Hunte 1999, Casazza & Ross 2008, Rudershausen et al. 2010, Tripp-Valdez et al. 2010, Farrell et al. 2014, Teffer et al. 2015), the fact that fishermen commonly target this habitat when angling for dolphinfish could have contributed to a positive bias toward *Sargassum*-associated prey recovered from dolphinfish stomachs. Other prey that contributed to the diverse foraging habits of dolphinfish in the US South Atlantic included several schooling fishes, such as smaller conspecifics, flying fishes, bullet tuna *Auxis* spp., and ommastrephid squids. Consumption of mesopelagic fishes most likely occurs at night, facilitated by prey fish vertical migrations toward surface waters as well as nocturnal movements into deeper water by dolphinfish predators (Merten et al. 2014). Large male dolphinfish have also been found to utilize open-water habitats independent of *Sargassum* mats (Rose & Hassler 1974), which may have contributed to the wide range in the sizes and types of prey consumed. The range of both absolute and relative prey sizes eaten by dolphinfish were broad and increased ontogenetically, producing a classic wedge-shaped distribution of prey body sizes as a function of predator size (Scharf et al. 2000, Juanes et al. 2002). A similar level of prey size diversity has been observed in dolphinfish diets throughout their global range (Olson & Galván-Magaña 2002, Young et al. 2010, Teffer et al. 2015).

Wahoo diets were almost exclusively piscivorous and the least diverse of the 4 predators examined. High reliance on small scombrids, particularly bullet and frigate tunas (*Auxis* spp.), suggests that wahoo specialize on this prey group as is true in other regions throughout their range (Manooch & Hogarth 1983, Vaske et al. 2003, Rudershausen et al. 2010, Perelman et al. 2017). Wahoo displayed a moderate degree of dietary plasticity by including a mixture of epipelagic and mesopelagic fishes, some *Sargassum*-associated fishes, and cephalopods. Indeed, we noted a seasonal increase in the importance of cephalopod prey during the spring and summer, including argonauts. These pelagic octopods are rarely captured in fishery surveys (Shea et al. 2017); however, their prevalence in wahoo and other large pelagic predator diets in the NWA (Staudinger et al. 2013, Teffer et al. 2015) indicates they are more abundant than previously thought or they are being selectively targeted by predators within this guild. Crustaceans were noticeably absent from the diets of wahoo. Manooch & Hogarth (1983) attributed this aspect of wahoo diets to the lack of gill rakers that would aid in reten-

tion of small prey and facilitate ram feeding. Wahoo were the largest predator examined and, perhaps unsurprisingly, consumed the largest prey sizes among the 4 species in this study. A recent study in Indo-Pacific waters found remarkably similar trends in predator–prey body sizes to those found in US South Atlantic waters (Perelman et al. 2017). Rapid swimming speeds combined with enhanced tooth morphology enable wahoo to sever prey items (e.g. Bemis et al. 2005, Grubich et al. 2008) and increase the ability of wahoo to capture and manipulate relatively large fish prey compared to tunas.

4.2. Resource overlap and niche separation

For the large pelagic fish predators in the US South Atlantic Bight ecosystem, dietary overlap was greatest among predators that consumed prey associated with *Sargassum* (dolphinfish and blackfin tuna) or that fed upon large schooling fishes (e.g. Scombridae) and cephalopod prey (yellowfin tuna and wahoo). Seasonal patterns of trophic overlap were most pronounced during spring, especially between yellowfin tuna and wahoo diets which were dominated by scombrid fishes, as noted in previous studies (Vaske et al. 2003, Rudershausen et al. 2010). Blackfin tuna and dolphinfish also exhibited high dietary overlap during spring, which was attributed to large contributions of flying fish and crustaceans. We hypothesize that dietary overlap during spring may be greater because of increased spatial overlap among predators that are restricted to the narrow bands of warmer water associated with the Gulf Stream Current. As summer progresses and the inner shelf waters warm, predator spatial distributions likely become more diffuse contributing to increased separation among dietary niches that may be aligned with species-specific thermal and depth preferences (e.g. Kleisner et al. 2010). Alternatively, the continued high reliance on scombrid fishes during summer by wahoo and yellowfin tuna may indicate these prey are widely available during the warmer seasons and/or strong patterns of selective feeding by these 2 predators. While each of the predators examined in this study are broadly considered opportunistic in their foraging habits, unique aspects of their behavior and morphology appear to drive dietary specialization within the available prey guilds. While fish prey occurred consistently in each of the predator diets (%FO = 73–95), the extent of piscivory and the relative importance of unique prey fish guilds and sizes contributed to diverse trophic niches.

The trophic patterns revealed in this study support the idea of a structured piscivore guild within the US South Atlantic ecosystem, including different forms of piscivory in the sense of the hierarchy proposed by Keast (1985) for small lake ecosystems. Fish that accelerate the onset of piscivorous feeding through phenological and morphological adaptations were termed 'specialist' piscivores, while fish that feed on other fishes only later in life were termed 'secondary' piscivores (Keast 1985). We contend that the extent of piscivory and specialization on unique fish prey groups supports at least 3 piscivore forms within the US South Atlantic pelagic ecosystem. Wahoo meet the definition of a 'specialist' piscivore with a diet consisting of almost exclusively fish prey, a high occurrence of relatively large prey (>20% of predator body size), and with a large contribution of a single prey group (Scombridae; *Auxis* spp.). In contrast, blackfin tuna appear to be 'secondary' piscivores with a much lower reliance on fish prey (<35% by mass and number), a narrower relative prey size range (vast majority of prey <10% of predator body size), and strong contributions of crustacean and molluscan prey to the diet. We propose that while not possessing the foraging habits of a 'specialist' piscivore, both dolphinfish and yellowfin tuna would still be best defined as 'primary' piscivores. Each relies heavily on fish prey (%FO = 78–90), but differ from wahoo in that they feed on a diverse assemblage of prey fishes with less reliance on a single group. Each of these predators also include moderate to considerable amounts of crustacean and molluscan prey in their diets, which vary more seasonally. Given observations of trophic niche segregation among sympatric pelagic predators in other systems (Young et al. 2010, Olson et al. 2016), piscivore structuring within pelagic ecosystems appears common and likely contributes to disparate trophic niches and reduced competition for shared prey resources.

4.3. Implications for ecosystem models and fishery management

Our findings provide valuable insight into the community structure and foraging ecology of large pelagic fishes in the US South Atlantic and represent essential baseline data for future studies of ecosystem structure and function. The temporal resolution and extent of the present study also highlighted dietary shifts among seasons and patterns of trophic overlap within seasons that could not be observed in

previous studies where sampling was more limited in temporal extent. The present study also identified key differences in diets between contemporary and historical studies and between the US South Atlantic and other sub-regions of the NWA, as well as on a global scale (Olson et al. 2016). Despite the fact that most fish predators were collected through fishery-dependent methods, a broad range of body sizes was sampled, with the largest individuals often approaching or exceeding published estimates of maximum size (Doray et al. 2004, Lessa & Duarte-Neto 2004, McBride et al. 2008, Schwenke & Buckel 2008). Focused study of the trophic ecology of juvenile life stages would be valuable to more fully quantify ontogenetic shifts in diet.

Ecosystem-based approaches to the management of marine resources enable trade-offs among alternative harvest strategies to be quantified simultaneously for their effects on fishery yields and ecosystem function. The foundation of these approaches lies in the connections among species that cause the impacts of harvest, and other human and environmental perturbations, to be felt throughout the ecosystem (Patrick & Link 2015). The most direct connections among species within an ecosystem occur through trophic pathways, specifically predator–prey interactions, and competition. In the US South Atlantic Bight, efforts have accelerated recently to implement ecosystem-based management approaches (http://safmc.net/fishery-ecosystem-plan-ii-south-atlantic-ecosystem/) through improvements to a previously developed trophic model (Ecopath with Ecosim) specific to the region (Okey & Pugliese 2001). These improvements prioritize the expansion of data collection (diet and life history information for predators and forage species) during existing and new survey platforms. The advantages of a well-informed food-web model can be realized through confident projections of the impacts of specific harvest strategies and/or policy options on trophic interactions and potential ecosystem consequences (e.g. Chagaris et al. 2015). Through removals of predators or prey, harvest practices can stimulate cascading effects within food webs (e.g. Casini et al. 2012) and impact important ecological mechanisms of population control (e.g. Steneck et al. 2013) at broad spatial scales. Pelagic marine ecosystems that support diverse fisheries and community assemblages encompass a complex set of species connections across several trophic levels. Our ability to predict ecosystem responses to changing climatic conditions or patterns of exploitation will depend largely on our level of understanding of these connections.

The role of key forage species as important drivers of ecosystem dynamics has become more widely appreciated (Pikitch et al. 2012, Rice & Duplisea 2014, Buchheister et al. 2017). Indeed, the plan to implement ecosystem-based fishery management approaches in the US South Atlantic Bight places considerable emphasis on identifying critical forage species (Okey et al. 2014). Despite the high diversity of prey taxa (63 unique prey families) found in predator diets and foraging patterns that support disparate trophic niches, a few fish (e.g. *Auxis* spp. and flying fish) and invertebrate prey (e.g. ommastrephid squids) contributed disproportionately to the diets of the pelagic predators examined in this study. We conclude that these prey are widely abundant and serve as key forage species in pelagic ecosystems of the NWA. Future studies that quantify patterns in the relative abundance of key prey groups would provide additional insights into whether prey availability or predator selective behavior best explains observed foraging patterns. The paucity of information on the biology and population dynamics of important prey guilds in the NWA (Carpenter 2002, ICCAT 2016) necessitates additional surveys to fully support ecosystem-based management within the region.

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