TROPHIC DYNAMICS OF PELAGIC FISHES IN THE U.S. SOUTH ATLANTIC INFERRED FROM DIET AND STABLE ISOTOPE ANALYSIS

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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 pelagic ecosystems, the functional role played by large pelagic predators is poorly understood, yet this knowledge is essential to the application of ecosystem based approaches to fisheries management. To assess the trophic structure of the pelagic community in the US South Atlantic, stomachs and muscle tissue samples were collected from blue marlin *Makaira nigricans*, wahoo *Acanthocybium solandri*, dolphinfish *Coryphaena hippurus*, yellowfin *Thunnus albacares* and blackfin tuna *T. atlanticus* through participation in organized fishing tournaments and cooperation with charter fishing fleets operating in the offshore waters of North and South Carolina from spring 2010 through fall 2013. Diet items were removed from stomachs, identified to lowest possible taxon, and sizes reconstructed when possible. Indices of relative prey mass and occurrence were used to describe the diets and to evaluate the potential for resource competition among predators. Analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes was performed on muscle and liver samples from predators as well as muscle samples and whole body samples of prey. Stomach contents revealed fishes as the most important prey by mass for all predators during all seasons. Dolphinfish-blackfin tuna and wahoo-yellowfin tuna exhibited high diet overlap overall and during seasons. Stable isotopic analysis indicated seasonal shifts in primary prey use and trophic position by dolphinfish, yellowfin and blackfin tuna. A trophic hierarchy, in which larger predators occupied the highest trophic positions, was observed throughout the spring and summer but not during the rest of the year. Overall, predator species foraged in similar habitats and relied on few dominant prey items such as bullet tuna, *Auxis* spp. and shortfin squid, *Illex illecebrosus*. These results offer valuable insight into the community

structure and foraging ecology of large pelagic fishes in the U. S. South Atlantic and provide baseline data for future ecosystem studies.

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INTRODUCTION

There is considerable debate among fisheries scientists and resource managers as to how decades of large-scale commercial fishing has altered and continues to alter the structure of marine ecosystems (Hilborn 2007; Murawski et al. 2007; Myers and Worm 2003; Worm et al. 2006; Worm et al. 2009). The selective removal of large fishes that act as apex predators (species that exert top-down control on their community) can elicit changes in food web dynamics and has the potential to affect biomass across multiple trophic levels (Essington et al. 2006; Larkin 1996; Pace et al. 1999; Pauly et al. 1998). The majority of modern stock assessment models remain focused on the tradeoff between sustainability and exploitation level for a single fishery resource. These models do not take into account ecological interactions, such as competition and predation, which can represent significant sources of variability in growth and natural mortality (Christensen et al. 1996; Harvey et al. 2008; Hollowed et al. 2000b; Link et al. 2002). During the past two decades, there has been a call for management practices that account for fishing-induced changes in ecosystem structure (Botsford et al. 1997), allowing for the incorporation of the indirect effects of fishing, such as changes in trophic structure and species composition of prey, when assessing population biomass of commercially important species and overall ecosystem health (Pauly et al. 2000). As such, ecosystem-based fisheries management (EBFM) approaches are being implemented more frequently in the form of multi-species population models (Cox et al. 2002; Hollowed et al. 2000a; Jurado-Molina et al. 2005). However, before ecosystem-based approaches can be employed routinely, detailed information is needed on the trophic structure and foraging ecology of the community in question.

Yellowfin tuna *Thunnus albacares*, blackfin tuna *T. atlanticus*, wahoo *Acanthocybium solandri*, dolphinfish *Coryphaena hippurus* and blue marlin *Makaira nigricans* are representative

of a suite of large predatory fishes within the pelagic ecosystem of the U.S. South Atlantic Bight. Relatively high energetic demands coupled with a highly migratory nature imply that these species have the potential to remove large amounts of lower level production from the marine food web (Cox et al. 2002; Essington et al. 2002). Collectively, this group supports highly valued commercial and recreational fisheries, with dolphinfish and yellowfin tuna being the top landed marine fish in North Carolina (North Carolina Division of Marine Fisheries landings statistics), which accounts for the majority of the harvest of these species along the U.S. east coast. As higher trophic level predators, these species may exert direct control over the abundance of prey fishes and invertebrates, and their removal has the potential to elicit a trophic cascade (Carpenter et al. 1985; Pace et al. 1999). Blue marlins are targeted by the recreational fishery in the region as well but only occur as by catch in some of the commercial fisheries. However, due to historically high incidence of by catch in the region combined with their slow growth and maturity, abundance of blue marlin in the region is considered low relative to historic levels (ICCAT 2011). It is unknown if the high harvest of dolphinfish and yellowfin tuna is due to increased abundance from a release from predation/competition with blue marlin as seen for apex predators in the north Pacific (Cox et al. 2002; Polovina et al. 2009) or a shift in effort by the regional fishing fleet. The potential for cascading top-down effects on pelagic food webs related to variation in the abundance of apex predators highlights the need for greater understanding of trophic dynamics within marine systems for effective ecosystem-based fisheries management.

Trophic analysis requires a comprehensive approach that evaluates both predator diet and trophic position in order to describe regional food webs accurately and enable an ecosystem approach to management (Cox et al. 2002). Describing fish diets based on the analysis of

stomach contents is standard practice in food web studies because it allows for the evaluation of predator-prey interactions through the direct observation of prey included in a predators diet (Chipps et al. 2007; Garvey and Chipps 2013; Pinkas et al. 1971). Several dietary indices can then be used to characterize the relative frequency of occurrence (%FO) of particular prey, their numerical importance (%N), and their contribution to total prey mass consumed (%M) (Hyslop 1980). However, each of these indices alone can sometimes provide a biased representation of diet, as %FO provides no indication of the relative amounts of prey, %N tends to overemphasize small, numerous prey, and %M can under represent the contribution of rapidly digested food items, and they can be impractical to compare among species. Also, these indices are calculated using data pooled across stomach samples to generate a single value for each prey type and thus, no estimate of variance is generated for the index making statistical comparison impossible (Chipps and Garvey 2007). Metrics that combine multiple dietary indices (e.g., index of relative importance [IRI]) can facilitate comparisons among species and studies, but they can be difficult to interpret. In addition, traditional diet studies typically only provide information about what a predator has eaten recently and, due to the relatively large data requirements, make it difficult to evaluate temporal and spatial feeding patterns (Estrada et al. 2005; Menard et al. 2007; Pinnegar and Polunin 1999; Revill et al. 2009). Stable isotope analysis is increasingly being used to compliment traditional diet studies in order to overcome some of the potential biases of stomach content analysis (Boecklen et al. 2011). Because of variable turnover rates in fish tissues, stable isotopes provide an integrated view of feeding over an extended time period, which can allow for better insights into the temporal and spatial feeding patterns of individual predators as well as overall trophic structure of marine systems (Menard et al. 2007; Olson et al. 2010; Revill et al. 2009). The trophic information obtained from stable isotope analysis is based on the assumption

that the stable isotopic composition of a predator is directly related to that of its prey (DeNiro and Epstein 1976), and can be measured by determining the ratios of naturally occurring isotopes in fish tissues.

Predators incorporate the isotopic signatures of their prey through the metabolic breakdown of ingested organic material. Due to excretion of unused organic material, indigestible prey parts (e.g., bones and scales), and the inherent discrimination against heavy isotopes in chemical reactions, not all isotopes are incorporated into the tissue of a consumer, so measured values become enriched relative to the previous trophic level. The isotopic composition of an individual will depend on its diet, habitat use, trophic level, and the isotopic signature at the base (primary producers) of a food web (Fry 2006; Olson et al. 2010; Post 2002). Ratios of the natural abundance of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are most commonly used to describe trophic relationships in food web studies (Fry 2006; Layman et al. 2007; Ramos and Gonzalez-Solis 2012). Values of $\delta^{13}C$ in predator tissues are similar to those of their prey and can be used to ascertain sources of primary production at the base of the food web (Deniro and Epstein 1978). An enrichment of 1‰ of the carbon isotope signature of predators relative to their food source is common in aquatic systems (DeNiro and Epstein 1976). Conversely, $\delta^{15}N$ values increase in a stepwise manner from prey to predator and can be used as a proxy for trophic position (DeNiro and Epstein 1981). A 3.4‰ enrichment of the heavy isotope of nitrogen is most commonly used in fish food web studies to represent a single trophic level increment (DeNiro and Epstein 1981; Post 2002). Coupling stable isotope analysis with traditional examination of stomach contents allows for a more comprehensive view, both spatially and temporally, of regional food webs and can afford the opportunity to evaluate species life history characteristics based on broader ecosystem functioning (Revill et al. 2009).

Furthermore, stable isotope analysis can be more efficient because it often requires less sampling time than traditional stomach content analysis because fish with empty stomachs can be included in the analysis (Garvey and Chipps 2013). However, stable isotope analysis can only identify trophic levels or functional groupings of prey and does not have the resolution to differentiate between unique prey types with similar isotopic values. Therefore, the examination of stomach contents should always accompany stable isotope analysis if prey resolution at the species level is desired (Revill et al. 2009).

The primary objective of this study was to provide the first comprehensive evaluation of the feeding ecology of multiple apex predators within the U.S. South Atlantic pelagic fish community. We employed an integrated approach using traditional stomach content analysis (SCA) coupled with stable isotope analysis (SIA) to describe the trophic dynamics of four key fish predators (yellowfin tuna, blackfin tuna, dolphinfish, and wahoo) within this pelagic ecosystem. Specifically, we attempted to: (1) describe the diet of each species using traditional SCA techniques and identify seasonal shifts in prey use; (2) examine the predator size – prey size relationships to identify size-based trophic niches; (3) evaluate the potential for competition among predators based on diet overlap; and (4) use stable isotope analysis to describe the trophic structure of the community. Other predators within the pelagic community (e.g., blue marlin) were sampled opportunistically but sample sizes did not allow for quantitative examination of their diets. Therefore, the diets of these predators were only described qualitatively and then incorporated into the stable isotopic characterization of the food web.

METHODS

Sample collection.—The principal species sampled included yellowfin tuna, blackfin tuna, wahoo and dolphinfish. Other species were sampled less frequently, and included blue marlin, bigeye tuna *Thunnus obesus,* little tunny *Euthynnus alletteratus*, king mackerel *Scomberomorus cavalla*, shortfin mako *Isurus oxyrinchus*, skipjack tuna *Katsuwonus pelamis*, and rainbow runner *Elagatis bipinnulata*. All species were sampled from commercial and recreational landings from the waters off North and South Carolina between April 2010 and October 2013. During the period April - July, and also the month of October, samples were collected exclusively from recreational harvests, mostly during state or privately organized fishing tournaments. During other months, samples were obtained from commercial fisheries and from recreational charter captains. For all recreational landings, fishing occurred during the daylight hours in continental shelf waters roughly between latitudes 31.5ºN and 36.25ºN. All fish were caught using hook and line gear trolling ballyhoo *Hemiramphus brasiliensis*, mullet (Mugilidae), spanish mackerel *Scomberomorus maculatus*, other bait, or artificial lures. The capture time and gear used for commercially landed fish was mostly not reported to us. For diet analysis, stomachs were cut below the esophagus and above the pyloric sphincter, removed from the predator, placed in plastic bags and frozen. For SIA, samples (~10 g) of epaxial muscle and liver were removed from all predators, placed on ice and later frozen until laboratory analysis could be performed. Additionally, fork length, sex, and any available capture information were recorded for each individual.

Stomach content analysis.—In the laboratory, stomachs were thawed and all prey items were removed and rinsed with deionized water. All prey items were first identified to the lowest

possible taxonomic classification, enumerated, blotted dry and weighed (wet weight [g]), and whenever possible, measured (mm) for total length (fish and shrimp), carapace width (crabs), or mantle length (squid). Digestion state was also estimated for each prey item using a 0 – 4 scale (0, indigestible; 1, no evidence of digestion; 2, < 50% digested; 3, > 50% digested; 4, only hard parts remained). Recovered prey were identified based on external morphology and comparisons with published references (Carpenter 2002; Gosner 1971). Hard parts (cephalopod and octopod beaks and fish otoliths) recovered from the stomachs were identified using taxonomic keys (Campana 2004) as well as reference collections. Once identified, hard parts and partial bodies were measured (lower rostral length or lower hood length for squid and octopods, respectively; caudal peduncle depth, eye diameter, and otolith diameter for fish prey) and prey size was reconstructed using published equations (Clarke 1986; Staudinger et al. 2009; 2013; Xavier and Cherel 2009) or equations generated from whole prey items recovered during this study.

For each predator species, diet was characterized using gravimetric, numeric, and occurrence indices calculated for each unique prey type. Pooling prey within and across stomachs may represent a case of pseudoreplication since, at least for prey recovered within the same stomach, prey items may not be independent replicates (Hurlbert 1984). Therefore, mean percent abundance ($\overline{\%N}$), mean percent mass ($\overline{\%M}$) were instead used, along with percent frequency of occurrence (%FO), to characterize the diets. The proportional composition by abundance and weight of each prey type was calculated separately for each predator stomach and then averaged over all stomachs with food for each predator species, following:

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

where P is the number of fish recovered with food in the stomach, Q is the number of prey types in all the samples, and N_{ij} is the number of prey type i in predator j. For mean percent mass:

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

where P and Q are defined as in equation 1 and W_{ij} is the mass of prey type i in predator j. For both %N and %M, variance was calculated as:

$$s^2_{N\ or\ M} = \frac{\left(\sum_{j=1}^{P}\left(\frac{N_{ij}}{\sum_{i=1}^{Q} N_{ij}}\right) - \overline{N_{ij}}\right)^2}{P-1} \quad (3)$$

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

$$\%FO = \frac{J_i}{P} \times 100 \quad (4)$$

where J_i is the number of individuals of predator J containing prey type i and P is the number of fish recovered with food in the stomach. Stomachs containing only prey items at a digestive state of 4 were excluded from $\overline{\%N}$ and $\overline{\%M}$ estimates because hard parts tend to accumulate in stomachs and may therefore represent multiple feeding events. Their inclusion in these estimates could result in a positive bias in the dietary importance of prey taxa with hard parts that are not easily digested or evacuated (Garvey and Chipps 2013). However, these stomachs were included when estimating %FO because the index is only based on presence/absence of a prey, rather than abundance or mass.

Predator-prey body size relationships.—Predator length-prey length analyses were only performed for yellowfin tuna, blackfin tuna, wahoo, and dolphinfish. Sample size was insufficient to characterize these relationships for the other predators in the study. Ratios of

predator length-prey length (PPR) were calculated for each predator using all measured and reconstructed sizes of recovered prey. PPR frequency distributions were generated and compared among predator species. Quantile regression was used to evaluate the ontogeny of size-based feeding habits of each of the four predators (Cade et al. 1999; Scharf et al. 2000; Scharf et al. 1998). Bivariate scatter plots were generated from body lengths of predators and prey, and the upper (90th and 95th quantiles) and lower (5th and 10th quantiles) boundaries as well as least-squares means were estimated. Sample size requirements suggested by Scharf et al. (1998) were applied to determine the appropriate upper and lower quantiles for boundary estimation for each predator species.

Dietary overlap.—Schoener's index (Schoener 1970) was used to estimate the degree of diet overlap among predators by calculating the proportion of defined prey categories utilized by each predator. To simplify the analysis, prey were first grouped into families (fish and molluscs) or orders (crustaceans) and then overlap indices were calculated based upon percent weight and percent frequency of occurrence values. Schoener's index is calculated as:

$$\alpha = 1.0 - 0.5 \times \sum |p_{ij} - p_{ik}| \quad (5)$$

where j and k are the two predator species being compared, p_{ij} is the contribution of prey type i to the total weight or frequency of occurrence of all prey eaten by predator j, and p_{ik} is the contribution of prey type i to the total weight or frequency of occurrence of all prey eaten by predator k. Values for α range from 0 (no overlap) to 1 (complete overlap) and values of 0.6 or greater are considered significant (Schoener 1970).

Stable isotope analysis.—Ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes were measured in epaxial muscle and liver samples from the predators and also in prey recovered from predator stomachs. For prey analyses, stable isotope ratios were estimated from either whole prey items or from muscle sub-samples collected in the same manner as for the predators. In preparation for analysis, all samples were first dried in an oven at 60ºC for approximately 48 h or until a constant weight was reached, and then homogenized using a mortar and pestle. Aliquots of each sample (0.5-0.6 mg) were weighed to the nearest 1000th, placed into tin cups, and then analyzed for $\delta^{13}C$, $\delta^{15}N$, and C:N by first flash-combusting samples in a Costech ECS4010 elemental analyzer and then analyzing the gas using a Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer (CFIRMS) located at the UNCW Center for Marine Science. Stable isotope abundances are reported in δ notation and expressed in terms of per mil (‰) deviation from a known standard using the following equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000 \quad (6)$$

where X is ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard materials used for carbon and nitrogen were Vienna Pee Dee Belemnite (VPDB) and atmospheric N2 (AIR), respectively. Measurement precision was < 0.2‰ for $\delta^{15}N$ and < 0.1‰ for $\delta^{13}C$ based on replicates of standards and fish samples across multiple runs.

Lipids in muscle and liver samples are depleted in ^{13}C relative to the proteins in the tissue (DeNiro and Epstein 1977; Post et al. 2007). Because of the variability in lipid content among individual fish, $\delta^{13}C$ values can be lower and vary widely among samples in which lipid has not been removed or accounted for, potentially causing misinterpretation of dietary shifts. *A priori* chemical extraction of lipids can alter $\delta^{15}N$ values (Pinnegar and Polunin 1999; Sotiropoulos et al. 2004) and require the sample to be analyzed twice (prior to extraction to determine $\delta^{15}N$ and

subsequent to extraction to measure $\delta^{13}C$; Sweeting et al. 2006). Mass balance equations can be used *a posteriori* to correct for lipids by incorporating the C:N ratio as a proxy for lipid content within the sample (Fry 2002; Logan et al. 2008). Previously published equations and model parameters from Logan et al (2008) were used to correct for lipid content in all predator and prey samples analyzed in this study. Species-specific parameters were not available for the species included in the present study, therefore model parameters were chosen from similar species when possible. Atlantic bluefin tuna (*Thunnus thynnus)* muscle and liver parameters were used for blackfin and yellowfin tuna, non-species specific fish liver and muscle parameters were used for all other predators and fish prey, and non-species specific invertebrate parameters were used for all invertebrate prey (Logan et al. 2008).

Linear regression was used to examine size-based patterns in estimated trophic position and foraging habitat by evaluating $\delta^{13}C$ and $\delta^{15}N$ as a function of body size (FL). Analysis of covariance (ANCOVA) was used to investigate seasonal shifts in trophic position ($\delta^{15}N$; dependent variable) using body size (FL) as a covariate. Trophic guilds within the pelagic community were visualized using cluster analysis of predator and prey $\delta^{13}C$ and $\delta^{15}N$ employing Ward's minimum variance method.

Trophic Position estimation— The trophic position of all species was evaluated based on nitrogen stable isotope data using the following equation:

$$TP = \lambda + \left(\frac{\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{base}}{\Delta_n}\right) \quad (7)$$

where λ is the trophic position of the organism used to estimate the $\delta^{15}N$ at the base of the food web ($\delta^{15}N_{base}$), Δ_n is the enrichment in ^{15}N per trophic level, and $\delta^{15}N_{secondary\ consumer}$ is the $\delta^{15}N$ of the organism for which trophic position is being estimated (Post 2002). For the species

chosen to represent the base of the food web, two important assumptions should be met: (1) the representative species inhabits the same habitat as the targeted species, and (2) that the species integrates the isotopic signature of the community over a sufficiently long temporal period to minimize potential effects of short-term variation (Post 2002). Rooker et al. (2006) investigated carbon sources within a pelagic food web in the Gulf of Mexico and estimated that 78% of the carbon supplied to the primary consumers was derived from particulate organic matter (POM), while the remainder could be attributed to *Sargassum* spp. production. The $\delta^{15}N$ of *Sargassum* (20% contribution) and POM (80% contribution) were selected to represent the base of the food web in the present study and was assigned a trophic level of 1.0 (Rooker et al. 2006). $\delta^{15}N$ of *Sargassum* (4.7‰) was directly measured from the diets of the predators and $\delta^{15}N$ of POM (4‰) was obtained from the literature (Montoya 2002), producing an estimated baseline $\delta^{15}N$ value of 4.14‰.

Niche width and overlap.—Stable isotope analysis provides a time integrated measure of dietary sources ($\delta^{13}C$ values of consumers match that of their prey) and trophic position ($\delta^{15}N$ increases from resource to consumer) within a food web that allows for the characterization of population niche space, referred to as isotopic niche (Bearhop et al. 2004; Newsome et al. 2007; Vander Zanden and Rasmussen 1999). When $\delta^{13}C$ and $\delta^{15}N$ values are plotted in two-dimensional space, each observation represents an individual diet and the space occupied by all observations, measured as the minimum convex hull total area (TA), represents the isotopic niche diversity of the population (Layman et al. 2007; Syväranta et al. 2013). Estimates of convex hull area are not coupled with variance estimates, and can be sensitive to small or uneven sample sizes (Layman et al. 2007). Therefore, Bayesian methods were also used to calculate standard ellipse area

(SEA), which is equivalent to standard deviations in univariate techniques (Jackson et al. 2011). The isotopic niche width and overlap metrics for the four focal predators were estimated using the Stable Isotope Bayesian Ellipses in R methods (Jackson et al. 2011) within the R statistical package SIAR (Parnell et al. 2010). To assess differences among species niche metrics, probability ranges of the means for each predator were estimated using 10^4 posterior draws of the standard ellipses (Jackson et al. 2011). Differences in niche width were also presented graphically as SEA (core area of niche) and TA (overall niche diversity). The overlap of SEA was calculated for each pair of species and compared qualitatively with the overlap indices calculated from the diet data.

RESULTS

Stomach content analysis—In total, 1,262 fish were examined for stomach content analysis between April 2010 and October 2013. All fish were sampled either in association with organized fishing tournaments or through cooperative efforts with charter and recreational fishing operations. Sampling was concentrated during late spring through early fall (April – October) because of the high amount of fishing effort during this period, but a small number of samples was collected during January through March; no samples were collected in either November or December (Fig. 1). The predators which dominated sampling included blackfin tuna (n = 285), dolphinfish (n = 457), wahoo (n = 239), and yellowfin tuna (n = 245; Table 1). Predator size ranges displayed good contrast, with the largest individuals often approaching or exceeding published estimates of maximum size, and the proportion of stomachs containing prey was high (60.4 - 93.7%, depending on predator species). Stomachs that were empty or only contained readily identifiable bait were excluded from the calculation of dietary indices. Fish prey were recovered most frequently from each of the predator species, as %FO ranged from 73.8 – 95.1% (Appendix Table A). Fish prey also accounted for the greatest fraction of prey mass for dolphinfish (81.8%), wahoo (92.7%), and yellowfin tuna (62.2%), with crustacean prey contributing the most mass to the diets of blackfin tuna ($\%M_{crustaceans}$ = 46.5%).

Stomatopoda were the single most important prey by mass ($\overline{\%M} = 9.52$), abundance ($\overline{\%N} = 9.66$) and frequency of occurrence (%FO = 27.3) for blackfin tuna but varied seasonally with the highest recorded values during the winter months (Figs. 2a, 3a, 4a). Flying fish (Exocoetidae*)* were the most abundant and contributed the most to mass of any fish prey recovered from the diets of blackfin tuna but only during the spring months (Fig. 4a). Other important prey items ($\overline{\%M}$ and $\%FO > 1$) for blackfin tuna consisted of mostly free swimming

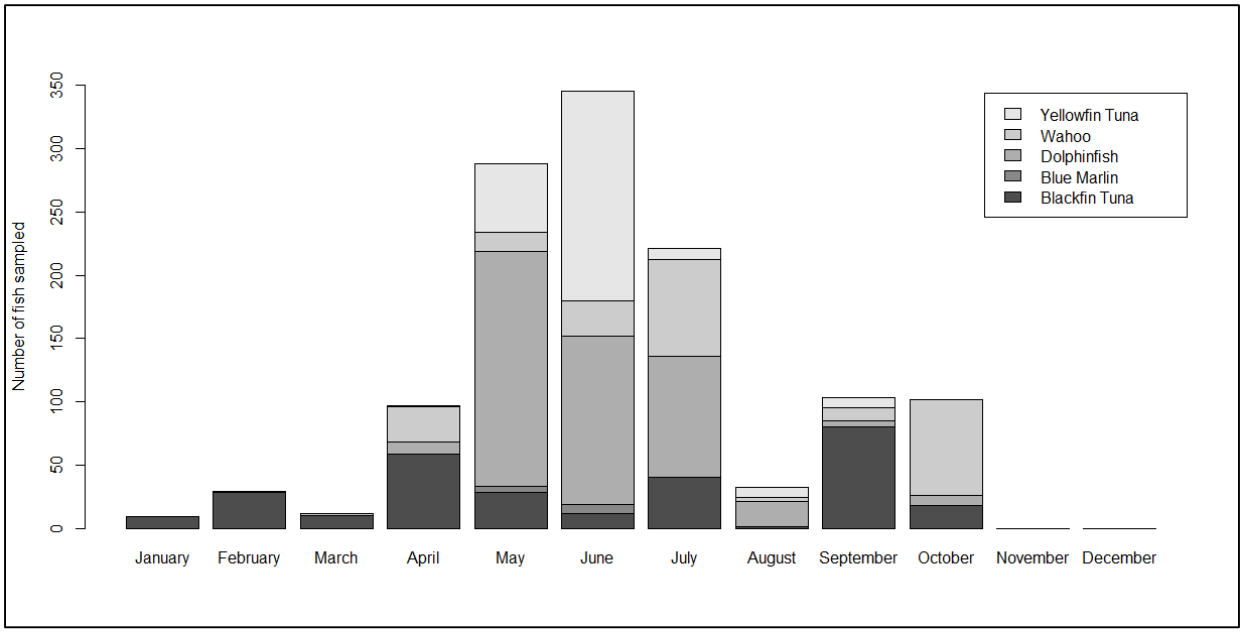

Figure 1. Number of predators sampled by month for diet and stable isotope analysis.

Table 1. Summary of fish sampled for diet and stable isotope analysis from North and South Carolina between April 2010 and October 2013 (N, number of fish collected; FL, fork length). Numbers in parentheses represent the percent of stomachs containing prey.

Species	N (%)	Min FL(cm)	Mean FL(cm)	Max FL(cm)
Auxis sp.	4 (100)	30.5	33.0	36.4
Barracuda	1 (100)		27.9	
Bigeye Tuna	2 (50.0)	121.9	148.6	175.3
Blackfin tuna	285 (93.7)	28.5	66.9	94.5
Blue Marlin	12 (75.0)	252.1	266.1	277.5
Dolphinfish	457 (83.2)	35.6	86.4	140.4
King Mackerel	1 (100)		118.5	
Little Tunny	8 (50.0)	58.6	71.1	81.4
Shortfin Mako	1 (100)		193.5	
Rainbow Runner	1 (100)		57.6	
Skipjack Tuna	7 (86.7)	54.8	56.8	58.5
Wahoo	239 (60.4)	91.0	130.5	177.0
Yellowfin tuna	245 (77.1)	46.6	94.9	140.7
	1263 (85.3)			

species of crustaceans in the orders Amphipoda and Isopoda, fish in the families Carangidae, Scombridae, Stromateidae, and Monacanthidae, and mollusks in the families Argonautidae, Ommastrephidae, Loliginidae, and Cavoliniidae.

Dolphinfish demonstrated the most diverse diet of any predator sampled with prey representing 109 genera in 46 families. Most of the important prey species recovered from the diets of dolphinfish are species known to associate with *Sargassum* algae and other floating debris (evinced by the high occurrence of *Sargassum* found in their stomachs [$\%FO = 29.14$]), except for scombrid fish, flying fish, shortfin squid *Illex illecebrosus* and longfin squid *Doryteuthis pealeii*. *Sargassum* associated fish and invertebrate species recovered from their diets include jacks (Carangidae), filefish (Monacanthidae), porcupinefish (Diodontidae), triggerfish (Balistidae), pufferfish (Tetraodontidae), other dolphinfish, and swimming crabs in the family Portunidae. Similar to blackfin tuna, flying fish were the most important piscine prey by mass ($\overline{\%M} = 19.18$), abundance ($\overline{\%N} = 12.84$) and frequency of occurrence (%FO = 22.89) for dolphinfish overall. Seasonally however, flying fish only dominated the diets during spring while Sargassum swimming crabs *Portunus sayi*, flying fish, round herring *Etrumeus teres*, jacks and filefish were of equal importance during the summer and jacks and filefish dominated in the fall (Figs. 2b, 3b, 4b).

Wahoo were chiefly piscivorous and displayed the least diverse diet among the predators sampled. Fish representing the family *Scombridae* (mainly *Auxis* spp.) contributed the most biomass (Fig. 2c), and were the most abundant (Fig. 3c) and frequent (Fig. 4c) in the diets during all seasons sampled. Paper nautiluses *Argonauta* spp., shortfin squid, Atlantic bird squid *Ornithoteuthis antillarum*, and longfin squid as well as flying fish, carangids, and diodonts were

of secondary importance to wahoo based on mass and occurrence indices and varied little by season (Figs. 3c; Figs. 4c).

Yellowfin tuna diets were similar to blackfin tuna, demonstrating a high occurrence of invertebrate and fish prey. Similar to wahoo, scombrid fish (mostly *Auxis* spp.) were also the most important prey by mass ($\overline{\%M} = 20.00$), abundance ($\overline{\%N} = 14.89$) and frequency of occurrence (%FO = 20.63) for yellowfin tuna overall. Amphipods occurred most frequently (%FO = 43.92) and contributed the most biomass ($\overline{\%M} = 10.59$) to the diet of yellowfin tuna relative to other crustaceans. Flying fish, monocanthids, carangids and herrings of the family Dussumieriidae as well as paper nautiluses and shortfin squid were also found to be important prey of yellowfin tuna based on mass and frequency of occurrence indices. During the spring months, scombrid fish and amphipods dominated the diets while crustaceans, scombrid fish and shortfin squid tended to dominate in the summer and flying fish and scombrid fish during the fall (Figs. 2d, 3d, 4d).

Predator-prey body size relationships.—Sample sizes of predator and prey lengths were sufficient to fit regression quantiles for blackfin tuna (n = 742), dolphinfish (n = 873), wahoo (n = 88), and yellowfin tuna (n = 450). Median (50^{th} quantile) prey size increased significantly (all P-values < 0.02) with predator size for each species (Fig. 5). With the exception of yellowfin tuna, each of the predator species demonstrated a broader range of prey sizes consumed with increasing body size, indicated by steeper slopes for the maximum prey sizes eaten (95^{th} quantile) relative to the median (Fig. 5; Table 2). Also, all species but wahoo showed moderate increases in minimum prey sizes eaten at larger predator body sizes, but the slopes were very shallow relative to changes in median and maximum prey sizes eaten. Prey length-predator

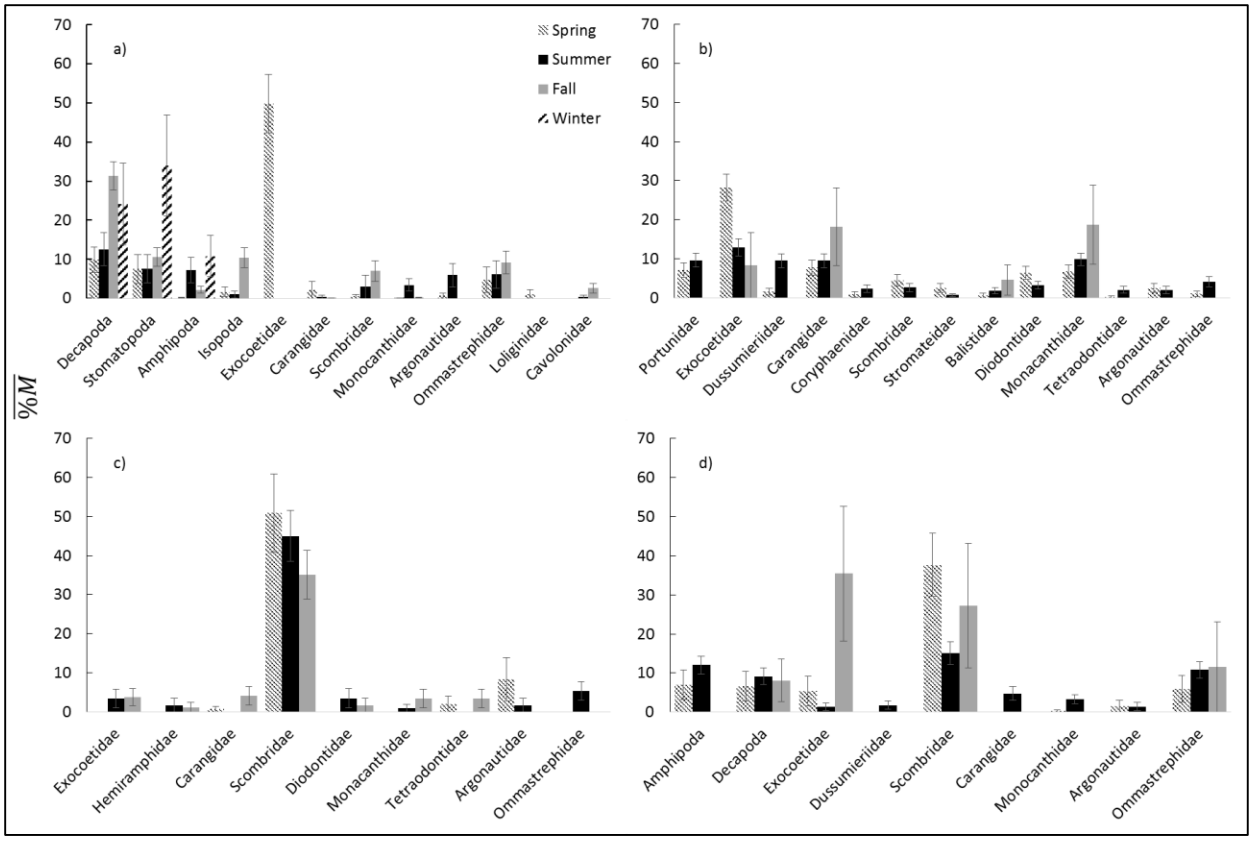

Figure 2. Mean percent mass ($\overline{\%M}$) of major prey orders and families by season in the diets of (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna. Error bars represent standard error (SE) of the means.

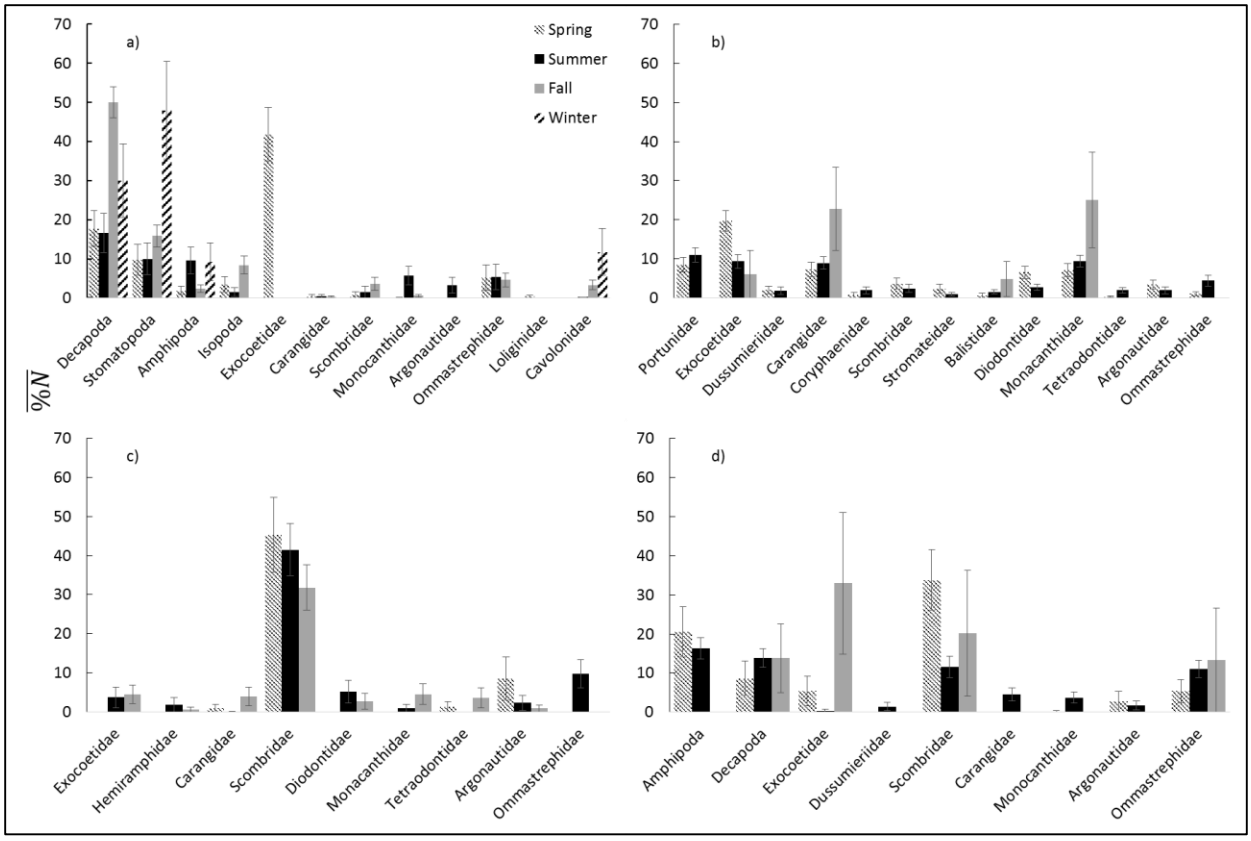

Figure 3. Mean percent abundance ($\overline{\%N}$) of major prey orders and families by season in the diets of (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna. Error bars represent standard error (SE) of the means.

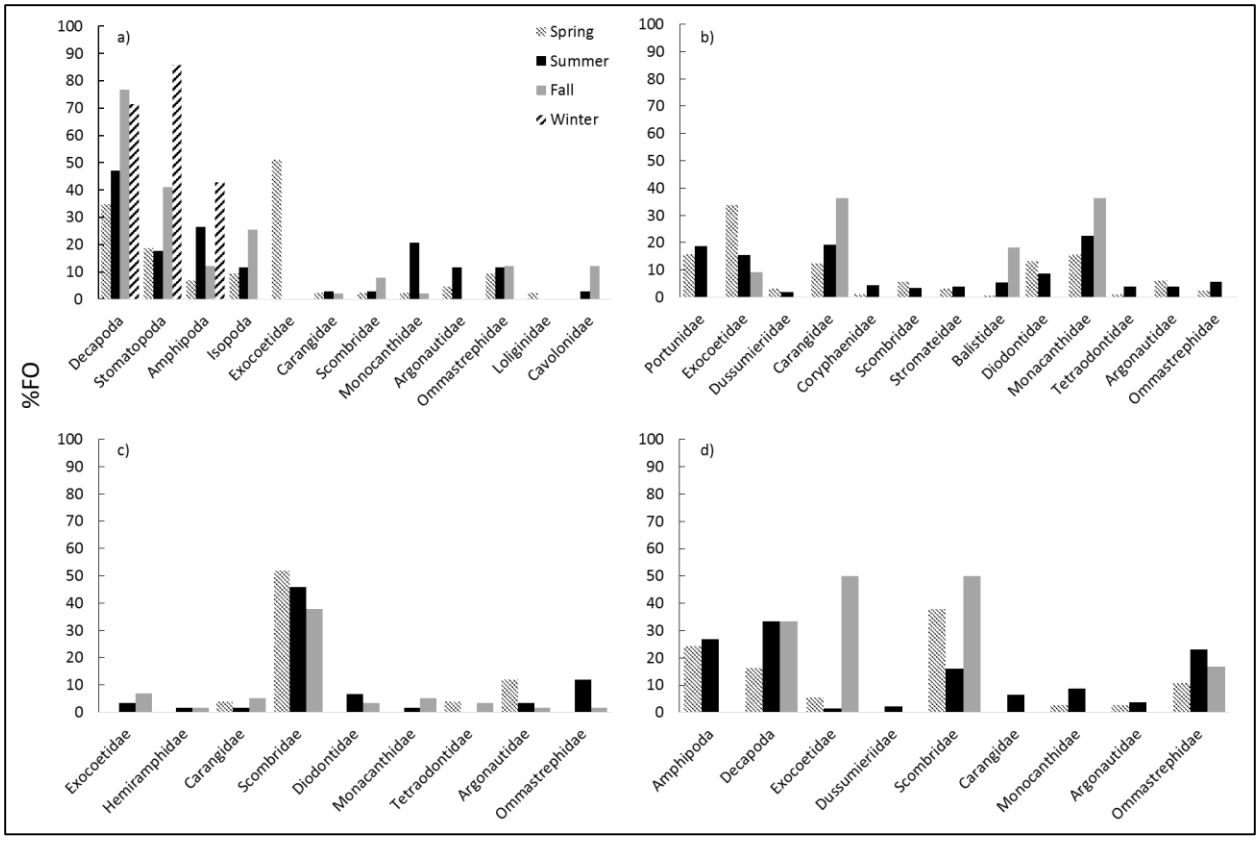

Figure 4. Percent frequency of occurrence (%FO) of major prey orders and families by season in the diets of (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna.

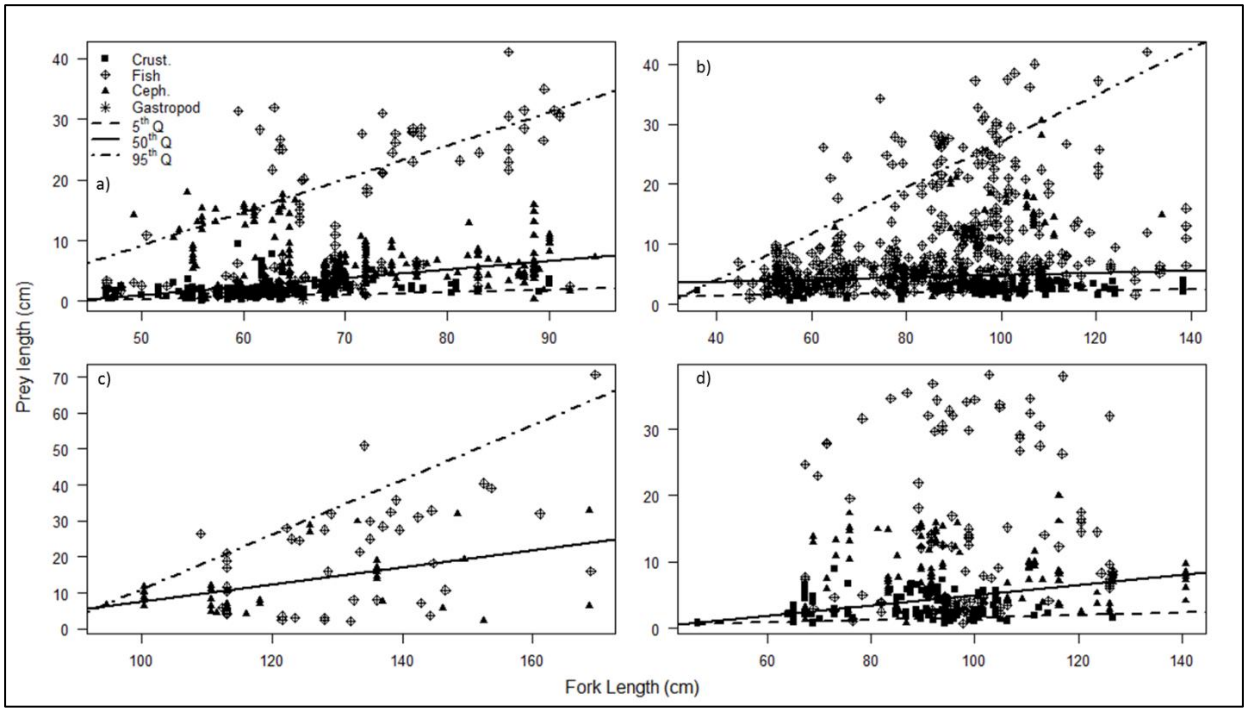

Figure 5. Lengths of prey (total length of fish, shrimp, amphipods and isopods; carapace width of crabs; mantle length of squid; body width of gastropods) recovered from predator diets as a function of predator fork length for (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna. Upper (95th quantile), lower (5th quantile), and median (50th quantile) are indicated on each panel when regressions were significant.

Table 2. Quantile regression parameter estimates for predator length-prey length relationships with boot strap estimates of standard error (SE). β_0 = regression constant; β_1 = slope; P = the significance of the regression. Only statistically significant ($P < 0.05$) parameter estimates are presented.

Quantile	β_0 (SE)	β_1 (SE)	P
Blackfin Tuna			
5^{th}	-1.780 (0.697)	0.040 (0.011)	< 0.001
50^{th}	-6.176 (0.790)	0.142 (0.013)	< 0.001
95^{th}	-18.506 (4.198)	0.553 (0.069)	< 0.001
Dolphinfish			
5^{th}	0.930 (0.930)	0.011 (0.011)	0.031
50^{th}	2.961 (0.606)	0.020 (0.008)	0.012
95^{th}	-11.331 (2.947)	0.385 (0.039)	< 0.001
Wahoo			
50^{th}	-16.122 (11.578)	0.238 (0.097)	0.016
95^{th}	-64.978 (23.294)	0.761 (0.197)	< 0.001
Yellowfin Tuna			
5^{th}	-0.323 (0.4153)	0.019 (0.005)	< 0.001
50^{th}	-2.715 (0.393)	0.078 (0.006)	< 0.001

length ratios (PPR) were generally similar among predator species with small prey (PPR ≤ 0.05) constituting the majority of prey sizes recovered from the diets (Fig. 6). Wahoo consumed prey that were nearly three times the size (mean prey length [PL] = 15.7cm) of prey consumed by blackfin tuna (mean PL = 5.2cm). Dolphinfish (mean PL = 7.2cm) and yellowfin tuna (mean PL = 7.4 cm) consumed more intermediate-sized prey. Fish were the largest prey consumed by blackfin tuna (mean PPR = 0.15), wahoo (mean PPR = 0.15), and yellowfin tuna (mean PPR = 0.14), while cephalopods represented the largest prey recovered from dolphinfish stomachs (mean PPR = 0.12).

Dietary overlap.—Schoener's dietary overlap index revealed significant overlap between blackfin tuna and dolphinfish, and also between wahoo and yellowfin tuna based on pooled prey percent mean mass data for all seasons, as well as in the spring (Table 3). Wahoo and yellowfin tuna were the only species that exhibited significant diet overlap during the summer and no overlap was observed for any predator combination in the fall. Significant dietary overlap was not observed between any predator species when frequency of occurrence or abundance was used as the metric.

Stable isotope analysis.— In total, 658 samples of muscle and 203 liver tissue samples were subsampled from among the predators that were examined for diet analysis and were analyzed for carbon and nitrogen stable isotopic composition. Additionally, 62 prey items representing 15 different families that were encountered in predator diets were analyzed. Individual isotopic values of predator muscle tissue ranged from -22.4‰ to -15.4‰ and from 7.1‰ to 14.0‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Similarly, liver samples ranged from -18.4‰ to -15.8‰ and

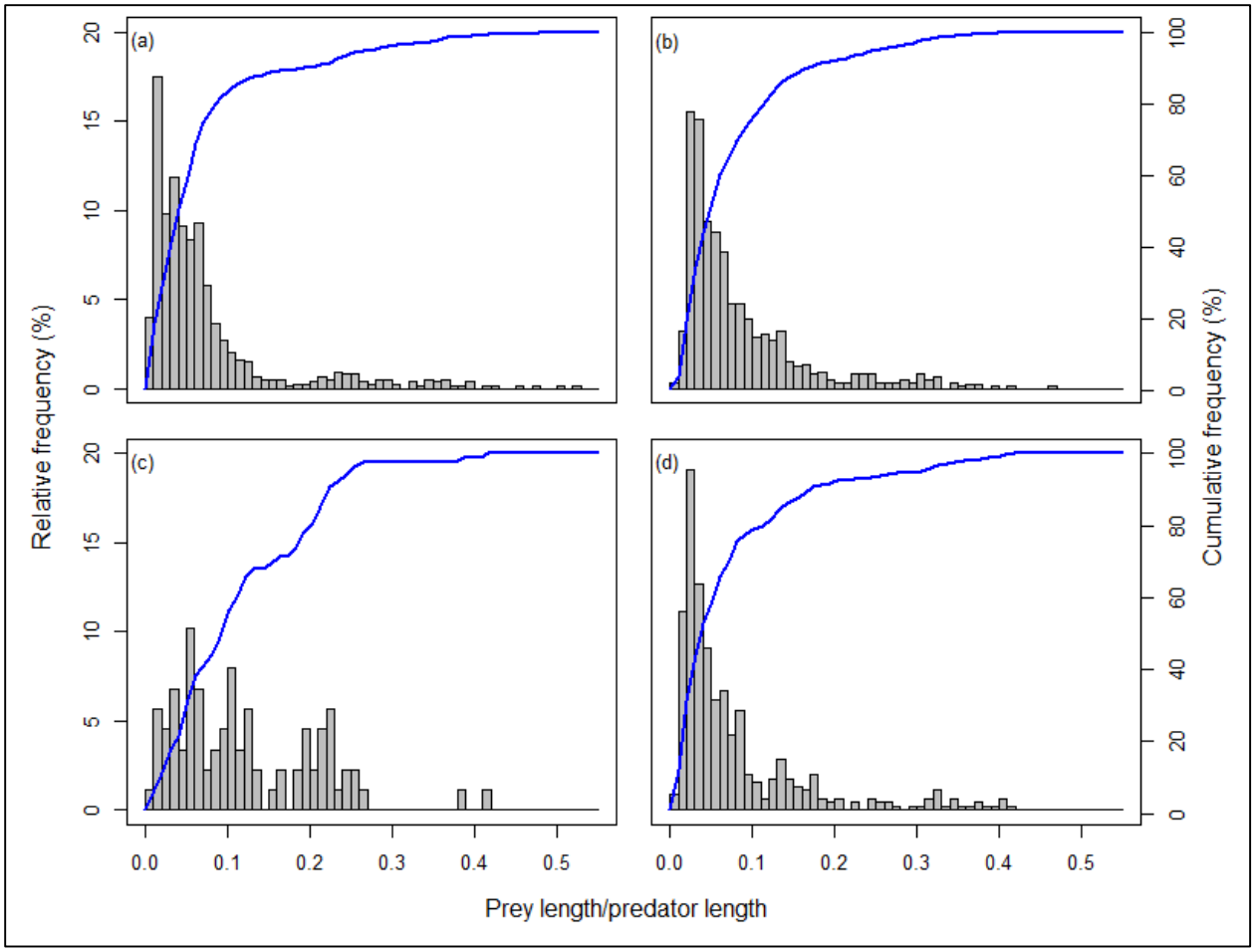

Figure 6. Relative and cumulative frequency distributions of prey size-predator size ratios (PPR) consumed by a) blackfin tuna, b) dolphinfish, c) wahoo, and d) yellowfin tuna. Bars and lines represent relative and cumulative frequencies, respectively, at 0.1% PPR intervals.
species except spring and fall samples for wahoo (Table 4).

Table 3. Schoener's index of dietary overlap between predators using prey mass data pooled across all seasons (All year sub-heading) and also within specific seasons. Index values > 0.60 were considered to represent significant overlap in diet and are denoted with an asterisk.

Season and Predator	Dolphinfish	Wahoo	Yellowfin Tuna
All year			
Blackfin Tuna	0.6491*	0.3716	0.4991
Dolphinfish		0.2885	0.3696
Wahoo			0.7675*
Spring			
Blackfin Tuna	0.6031*	0.0126	0.0274
Dolphinfish		0.0073	0.0363
Yellowfin Tuna			0.9439*
Summer			
Blackfin Tuna	0.2704	0.3363	0.3848
Dolphinfish		0.2237	0.2734
Wahoo			0.6470*
Fall			
Blackfin Tuna	0.0055	0.5015	0.5216
Dolphinfish		0.0266	0.2291
Wahoo			0.3937

from 6.4‰ to 11.5‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Mean $\delta^{13}C$ values in liver tended to be slightly more depleted relative to muscle, with the exception of dolphinfish (Table 4). Muscle tissue was also more enriched in nitrogen compared to liver tissue for all predators. Individual isotopic values of prey ranged from -19.9‰ to -14.7‰ and from 2.8‰ to 8.9‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Mean liver $\delta^{13}C$ values varied significantly among seasons in blackfin tuna ($\chi^2 = 9.664$, $P = 0.022$; Fig. 7a), wahoo ($\chi^2 = 12.470$, $P = 0.002$; Fig. 7c) and yellowfin tuna ($\chi^2 = 6.407$, $P = 0.041$; Fig. 7d), with the most enriched values observed in the fall. Blackfin tuna was the only predator that demonstrated significantly different muscle $\delta^{13}C$ ($\chi^2 = 17.894$, $P < 0.001$) and $\delta^{15}N$ ($\chi^2 = 49.420$, $P < 0.001$) values among seasons (Fig. 8a). Isotopic carbon ratios ($\delta^{13}C$) in muscle tissue increased significantly with increasing body size for blackfin tuna ($r^2 = 0.08$, $P < 0.001$; Fig. 9a) and dolphinfish ($r^2 = 0.20$, $P < 0.001$; Fig. 9e). Isotopic nitrogen ratios ($\delta^{15}N$) of muscle increased significantly with increasing body size for blackfin tuna ($r^2 = 0.68$, $P < 0.001$; Fig. 9b), dolphinfish ($r^2 = 0.07$; $P = 0.005$, Fig. 9f), and wahoo ($r^2 = 0.46$, $P < 0.001$; Fig. 9j), but significantly decreased in liver for yellowfin tuna ($r^2 = 0.11$, $P < 0.042$; Fig. 9n). No size dependence for carbon and nitrogen in the liver was observed (Fig. 9). ANCOVA results indicated that $\delta^{15}N$ values within liver tissue varied among seasons for wahoo ($F_{3,65} = 3.732$; $P = 0.015$) and yellowfin tuna ($F_{3,35} = 5.593$; $P = 0.003$). Mean TP estimated from $\delta^{15}N$ values ranged from 3.6 (Rainbow runner and fall Blackfin Tuna) to 5.3 (Little Tunny) within muscle tissue samples and from 4.6 (spring Yellowfin Tuna) to 5.9 (fall Wahoo) within liver tissue samples (Table 4). Across prey species, mean TP ranged from 1.7 (Carangidae and Stromateidae) to 3.9 (Ommastrephidae) (Table 5).

There was considerable isotopic overlap among and within predator species in both $\delta^{13}C$ and $\delta^{15}N$ values observed in the muscle tissue samples. For each of the four primary species studied, blackfin tuna, dolphinfish, wahoo, and yellowfin tuna, mean $\delta^{13}C$ and $\delta^{15}N$ values varied

< 2‰ in all cases (Table 4). Other predator species with limited sample sizes demonstrated similar $\delta^{13}C$ ranges, but $\delta^{15}N$ values varied more (~4‰; Table 4). Despite low interspecific variability, predators grouped into three guilds based on isotopic differences in carbon and nitrogen (Fig. 10). The first group contained false albacore, bigeye tuna, and mako shark, which were the species demonstrating the highest $\delta^{15}N$ values. Rainbow runner, dolphinfish, yellowfin tuna, king mackerel, and skipjack tuna occupied one of the remaining groups, while blue marlin, blackfin tuna, and wahoo were grouped together (Fig. 10). At the community level, predator and prey species generally grouped into four trophic guilds (Fig. 11). Small prey species often associated with floating macroalgae (*Sargassum* spp.) formed the trophic guild demonstrating the lowest mean $\delta^{15}N$ values. This guild included many prey families which were also found to be important in the diets of many of the predators including Carangidae, Diodontidae, Monacanthidae, and Tetraodontidae (Fig. 11). The next higher prey guild included fish and invertebrate taxa that consisted of larger genera not typically associated with *Sargassum* spp., and displayed relatively intermediate $\delta^{13}C$ and $\delta^{15}N$ values (Table 5). Prey in this guild were also found to be important in the diets of most predators and included the two prey types (*Auxis* spp. and Exocoetidae; Fig. 11) that occurred most frequently and contributed most to predator dietary mass. Conspecific prey of dolphinfish and yellowfin tuna were also grouped in this guild (Fig. 11). The last two trophic guilds were very similar to the guilds identified from the grouping of $\delta^{13}C$ and $\delta^{15}N$ values found in predator muscle tissue samples, but with the inclusion of Ommastrephidae squid grouped closely with blue marlin, blackfin tuna, and wahoo (Fig. 11).

Niche width and overlap.—The isotopic niche, measured as the standard ellipse area (SEA) and the total area of the convex hull (TA) of $\delta^{13}C$ and $\delta^{15}N$ values of muscle for all predator pooled across seasons was largest for dolphinfish (SEA = 2.29‰^{2}, TA = 12.72‰^{2}; Fig. 12a, 13a).

Standard ellipse area was similar among blackfin tuna (SEA = 1.00‰^{2}), wahoo, (SEA = 0.92‰^{2}), and yellowfin tuna (SEA = 1.08‰^{2}), but total area varied among the species with blackfin tuna having the next largest (TA = 9.40‰^{2}), followed by yellowfin tuna (TA = 7.31‰^{2}) and then wahoo (TA = 4.58‰^{2}; Fig. 12a, 13a). Seasonally, niche area did not vary among predators (Fig 12b-d, 13b-d). Estimated niche overlap of the ellipse areas was computed between all pairs of predator species and detected a high probability of overlap for blackfin tuna and dolphinfish, dolphinfish and wahoo, and dolphinfish and yellowfin tuna from isotopic values of muscle pooled across all seasons (Table 6).

Table 4. Sample sizes of predator muscle and liver tissue analyzed for stable isotopes, along with the isotopic signatures for $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD), and the estimated trophic position (TP) (mean ± SD).

Predator	Muscle				Liver			
	N	$\delta^{13}C$	$\delta^{15}N$	TP	N	$\delta^{13}C$	$\delta^{15}N$	TP
Blackfin Tuna	207	-16.8 ± 0.5	10.3 ± 0.9	3.9 ± 0.4	64	-17.1 ± 0.5	10.0 ± 0.7	5.5 ± 0.5
Spring	68	-16.7 ± 0.6	10.9 ± 1.0	4.2 ± 0.5	25	-17.2 ± 0.7	9.1 ± 1.0	5.2 ± 0.5
Summer	52	-16.9 ± 0.7	10.2 ± 1.2	3.9 ± 0.6	19	-15.5 ± 0.4	9.1 ± 1.0	5.2 ± 0.5
Fall	68	-16.8 ± 0.3	9.7 ± 0.8	3.6 ± 0.4	15	-16.9 ± 0.5	9.4 ± 0.8	5.1 ± 0.6
Winter	19	-16.5 ± 0.3	11.0 ± 0.9	4.3 ± 0.4	5	-17.1 ± 0.1	9.8 ± 0.7	5.4 ± 0.5
Dolphinfish	112	-17.0 ± 0.9	9.8 ± 1.0	3.7 ± 0.5	29	-12.6 ± 0.8	9.0 ± 0.8	4.7 ± 0.6
Spring	52	-17.0 ± 0.6	10.0 ± 1.0	3.8 ± 0.4	14	-12.5 ± 1.0	8.9 ± 0.8	4.7 ± 0.6
Summer	55	-17.1 ± 1.1	9.7 ± 1.0	3.6 ± 0.5	15	-12.6 ± 1.4	9.0 ± 0.8	4.7 ± 0.6
Fall	5	-16.6 ± 0.7	10.5 ± 0.8	4.0 ± 0.4				
Wahoo	201	-16.7 ± 0.5	10.3 ± 0.9	3.9 ± 0.4	70	-17.1 ± 0.5	10.0 ± 0.7	5.5 ± 0.5
Spring	33	-16.7 ± 0.3	10.1 ± 1.1	3.8 ± 0.5	6	-17.2 ± 0.2	10.4 ± 0.7	5.8 ± 0.6
Summer	97	-16.7 ± 0.3	10.3 ± 0.9	3.9 ± 0.4	54	-17.2 ± 0.4	9.9 ± 0.6	5.4 ± 0.5
Fall	70	-16.8 ± 0.7	9.7 ± 0.8	4.0 ± 0.3	10	-16.6 ± 0.6	10.5 ± 0.5	5.9 ± 0.4
Winter	1	-16.9	10.1	3.9				
Yellowfin Tuna	111	-17.0 ± 0.5	9.6 ± 0.7	3.6±0.4	39	-17.7 ± 0.5	9.1 ± 0.7	4.8 ± 0.5
Spring	31	-17.1 ± 0.4	9.7 ± 0.8	3.7±0.4	13	-17.9 ± 0.3	8.8 ± 0.4	4.6 ± 0.3
Summer	73	-17.0 ± 0.5	9.5 ± 0.7	3.6±0.3	24	-17.6 ± 0.5	9.2 ± 0.6	4.9 ± 0.5
Fall	7	-16.7 ± 0.4	9.7 ± 0.7	3.6±0.4	2	-17.0 ± 0.6	10.3 ± 0.3	5.8 ± 0.2
Bigeye Tuna	2	-16.4 ± 0.1	12.4 ± 0.5	4.9 ± 0.2				
Blue Marlin	10	-16.5 ± 0.6	10.7 ± 0.6	4.1 ± 0.3	1	-18.2	8.9	4.7
Little Tunny	6	-17.0 ± 0.4	13.2 ± 0.7	5.3 ± 0.3				
King Mackerel	1	-16.5	9.4	3.5				
Mako	1	-17.5	12.3	4.9				
Rainbow Runner	1	-17.3	9.7	3.6				
Skipjack Tuna	7	-17.0 ± 0.5	9.4 ± 0.6	3.5 ± 0.3				

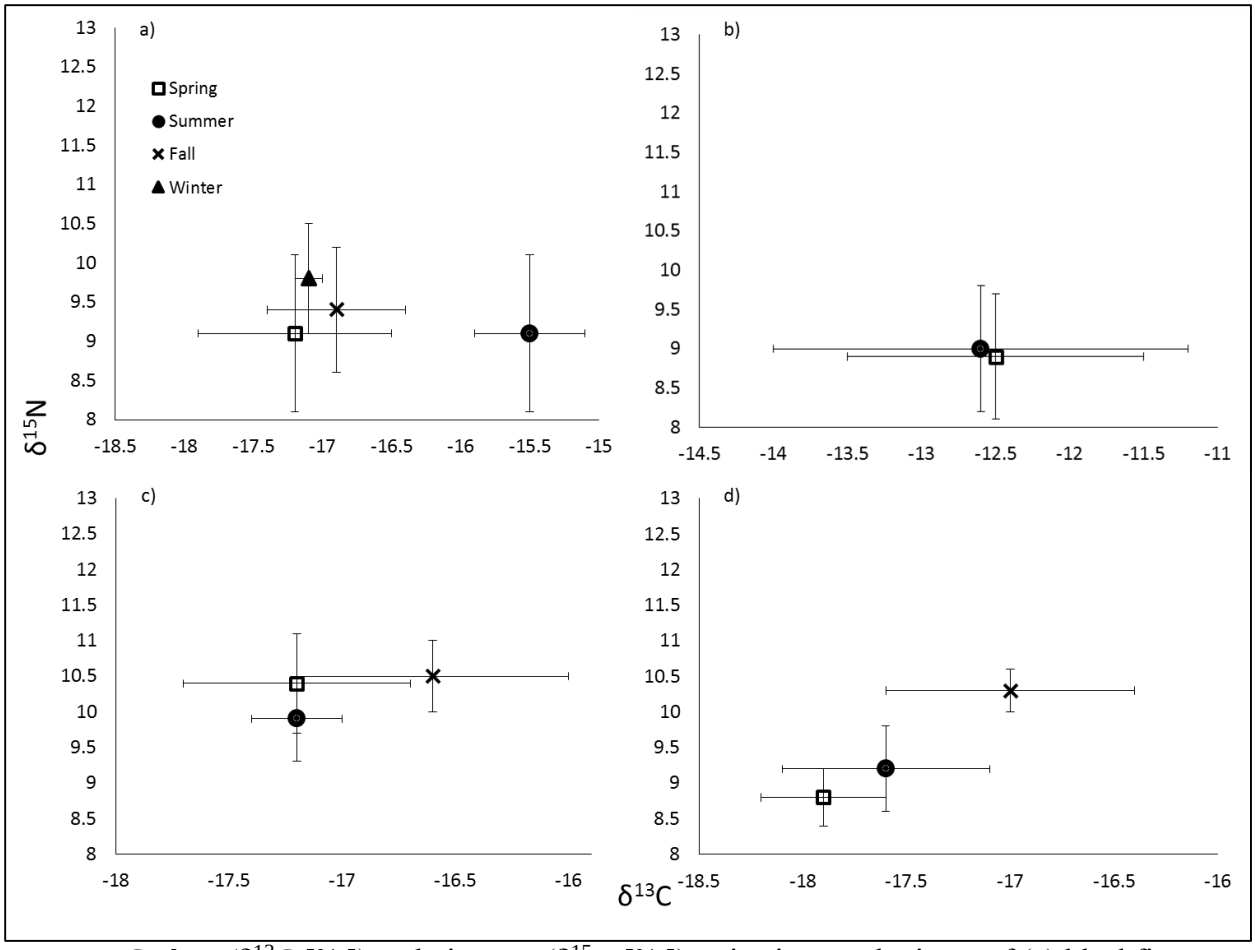

Figure 7. Carbon ($\delta^{13}C$ [‰]) and nitrogen ($\delta^{15}N$ [‰]) ratios in muscle tissue of (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna by season. Each symbol represents mean stable isotopic values with ± 1 standard deviation error bars.

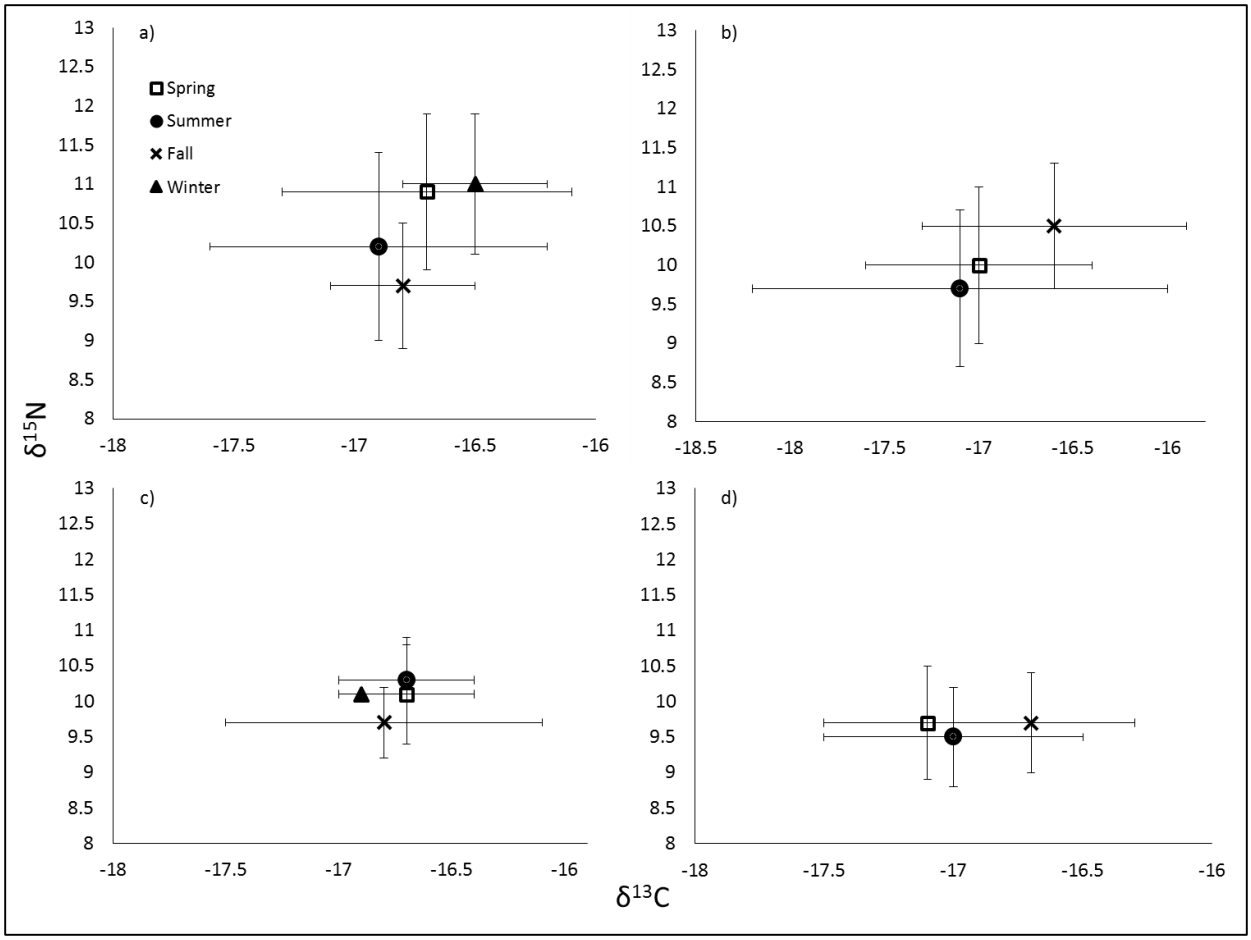

Figure 8. Carbon ($\delta^{13}C$ [‰]) and nitrogen ($\delta^{15}N$ [‰]) ratios in liver tissue of (a) blackfin tuna, (b) dolphinfish, (c) wahoo, and (d) yellowfin tuna by season. Each symbol represents mean stable isotopic values with ± 1 standard deviation error bars.

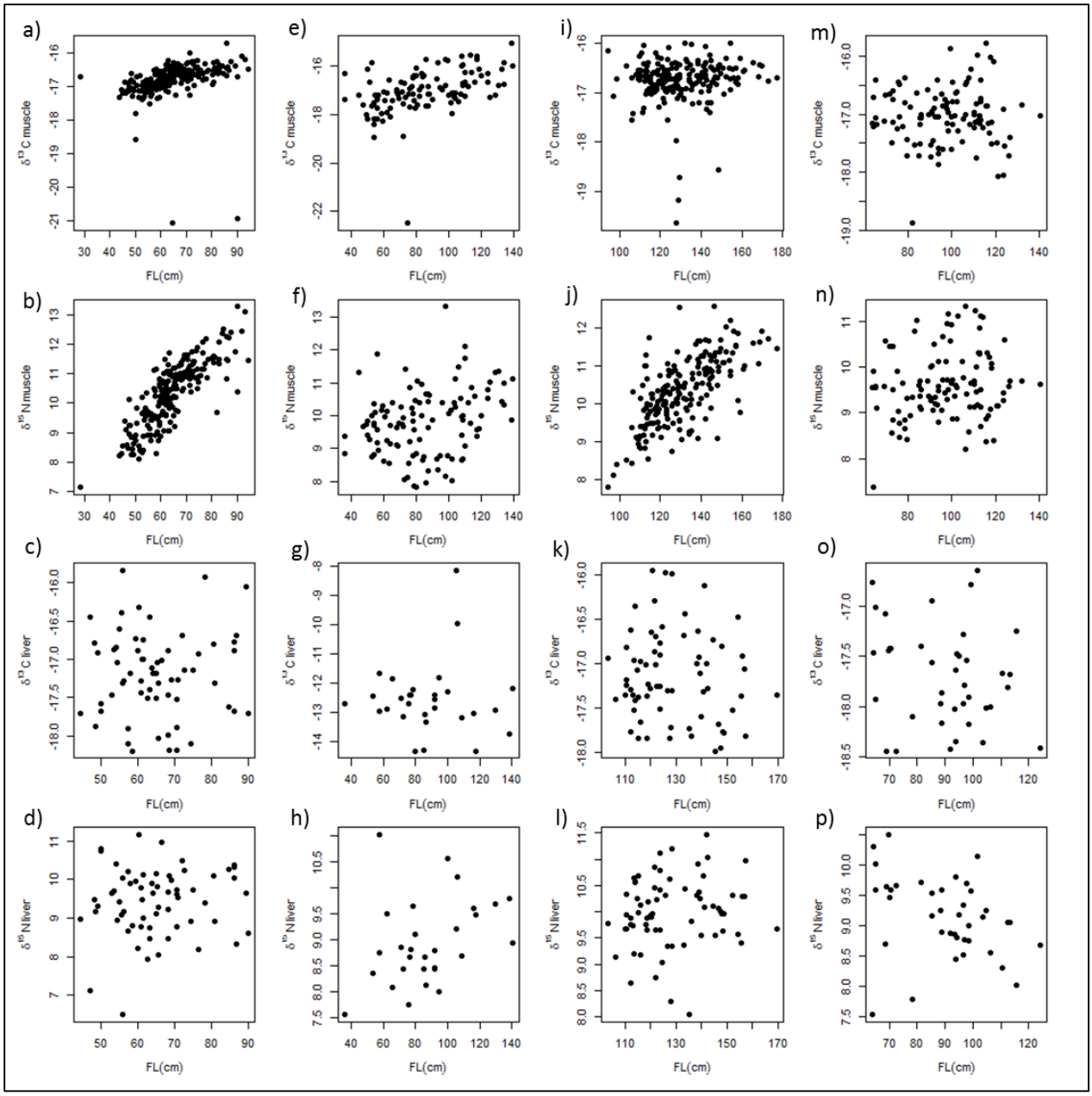

Figure 9. Isotope values of muscle tissue (δ^{13}C muscle [‰]; δ^{15}N muscle [‰]) and liver tissue (δ^{13}C liver [‰]; δ^{15}N liver [‰]) relative to body size for (a-d) blackfin tuna, (e-h) dolphinfish, (j-l) wahoo, and (m-p) yellowfin tuna.

Table 5. Families and species of recovered prey analyzed for stable isotopes, the predator species from which samples were recovered, and the number of prey sampled. BFT = Blackfin tuna; BM = Blue marlin; DOL = Dolphinfish; WAH = Wahoo; YFT = Yellowfin tuna. Tissue = tissue type analyzed. $\delta^{13}C$, $\delta^{15}N$, and trophic position (TP) are each mean ± SD.

Prey	Predator	Tissue	$\delta^{13}C$	$\delta^{15}N$	TP
Argonautidae *Argonauta sp.*	DOL = 3	Mantle	-18.2±1.2	8.0±0.2	2.9±0.1
Ommastrephidae *Illex illecebrosus*	BFT = 2; YFT = 2	Mantle	-17.2±0.5	10.3±0.8	3.9±0.4
Atherinopsidae *Menidia menidia*	DOL = 2	Muscle	-17.2±0.2	6.6±0.6	2.2±0.2
Exocoetidae	BFT = 2; DOL = 8	Muscle	-17.0±0.3	7.9±1.2	2.8±0.6
Dussumieriidae *Etrumeus teres*	DOL = 1	Muscle	-18.5	6.3	2.0
Carangidae *Selene vomer; Seriola zonata*	DOL = 3	Whole	-17.4±0.0	5.6±0.4	1.7±0.2
Coryphaenidae *Coryphaena hippurus*	DOL = 3	Muscle	-17.5±0.5	8.3±0.9	3.0±0.4
Gempylidae *Gempylus serpens*	WAH = 2	Muscle	-17.8	7.0±0.0	2.4±0.0
Scombridae *Auxis sp.*	BFT = 1; BM = 2; DOL = 3; WAH = 3; YFT = 2	Muscle	-17.9±0.4	9.0±0.9	3.3±0.4
Katsuwonus pelamis	BM = 1	Muscle	-17.3	9.0	3.3
Thunnus albacares	YFT = 1	Muscle	-17.5	8.7	3.2
Stromateidae *Peprilus paru*	DOL = 1	Whole	-19.4	5.6	1.7
Syngnathidae *Hippocampus erectus*	DOL = 4	Whole	-18.2±0.2	6.7±0.0	2.2±0.0
Diodontidae *Diodon holocanthus*	DOL = 3	Whole	-17.8±0.4	7.1±0.3	2.4±0.2
Monacanthidae *Aluterus monoceros; A. scriptus; Cantherhines pullus; Stephanolepis hispidus; S. setifer*	DOL = 5; YFT = 1	Muscle	-18.1±0.4	7.0±1.0	2.4±0.5
Tetraodontidae; *Lagocephalus sp.*	DOL = 1	Muscle	-17.4	6.6	2.2
Portunidae; *Portunus sayi*	BFT = 2; DOL = 2	Whole	-17.5±0.8	8.9±0.6	3.3±0.3

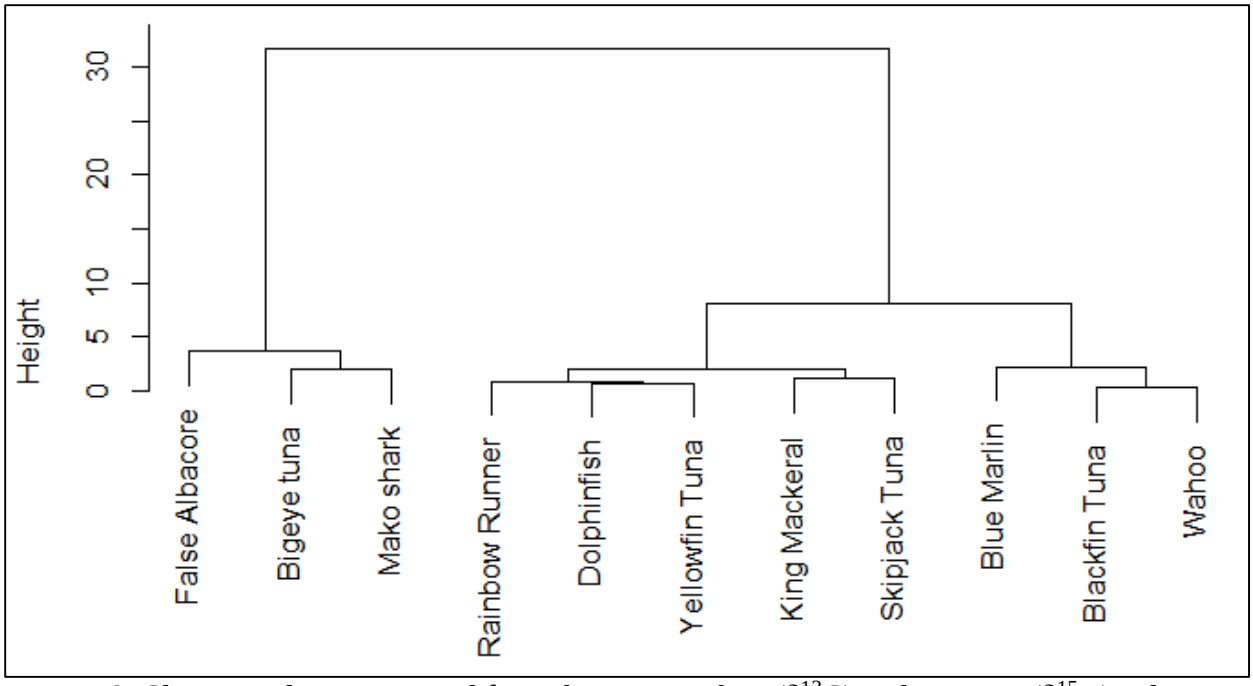

Figure 10. Cluster analysis generated from the mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in the muscle tissue of all predators sampled.

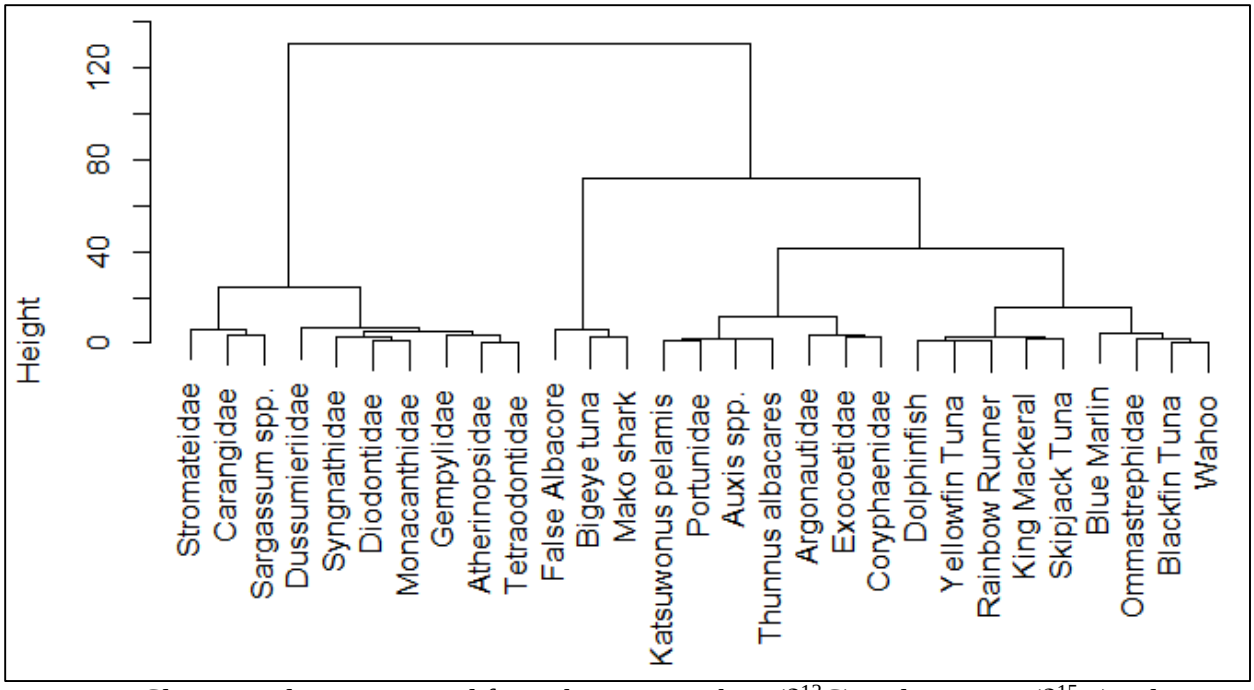

Figure 11. Cluster analysis generated from the mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in the muscle tissues of all predators and prey recovered from the diets of those fish.

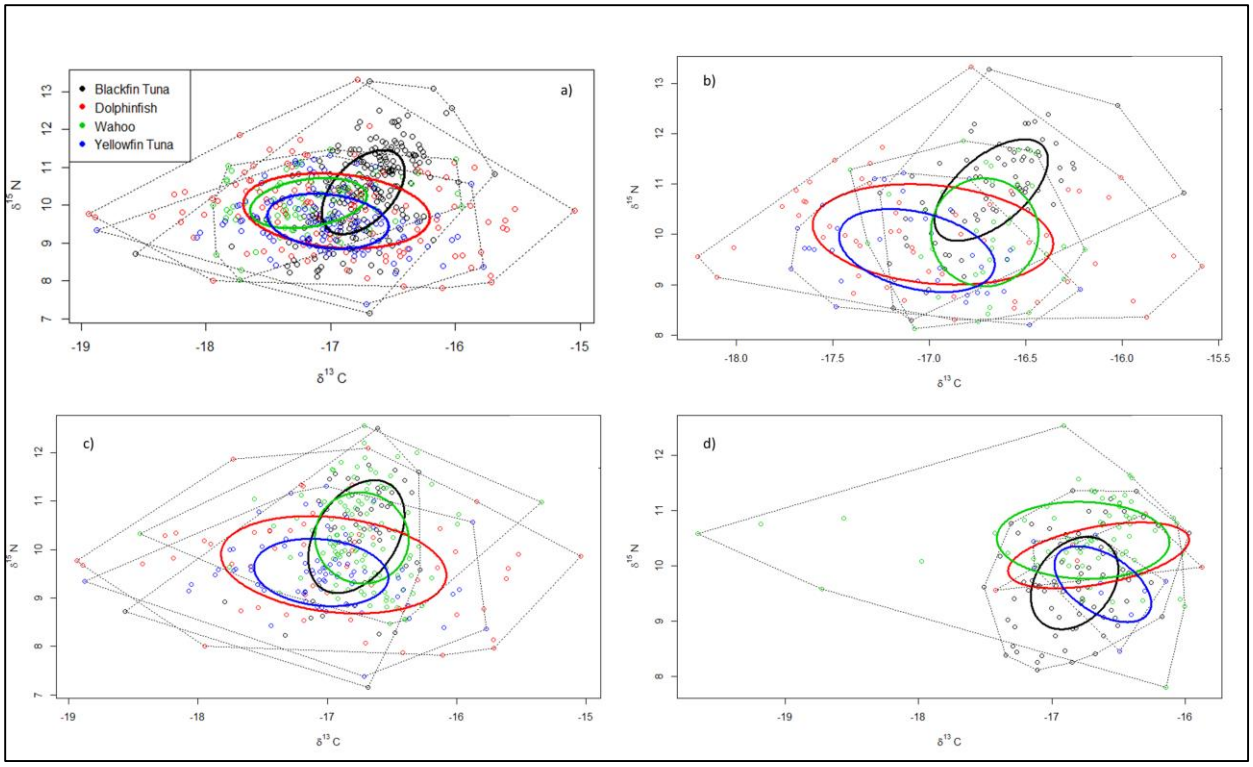

Figure 12. Convex hulls (dashed lines) encompassing all data points and standard ellipses (solid lines) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in the muscle of blackfin tuna, dolphinfish, wahoo, and yellowfin tuna during the (a) all seasons, (b) spring, (c) summer, and (d) fall.

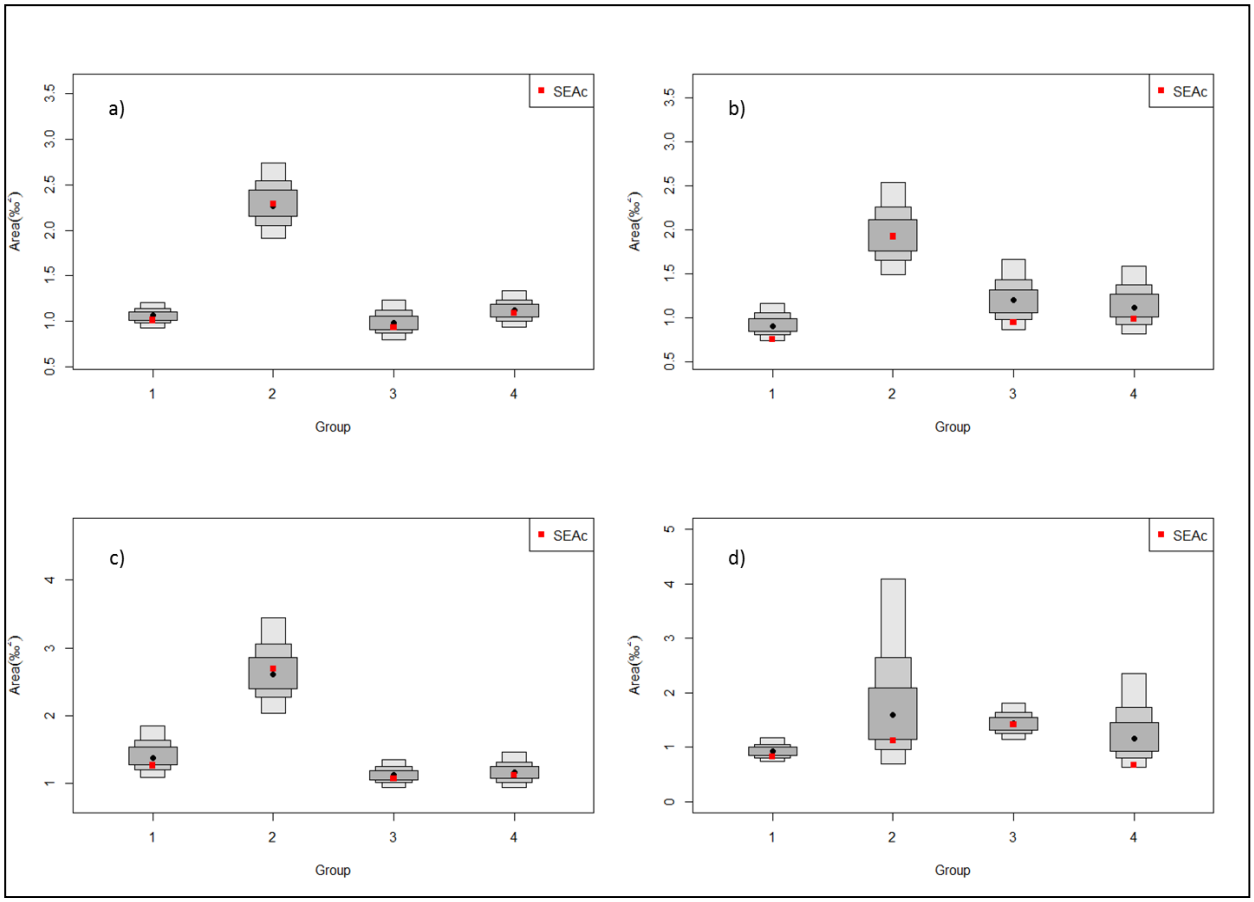

Figure 13. Bayesian credible interval estimates of standard ellipse area (SEA) and standard ellipse area estimates corrected for small sample size (SEAc) of (1) blackfin tuna, (2) dolphinfish, (3) wahoo, and (4) yellowfin tuna for (a) all seasons, (b) spring, (c) summer, and (d) fall.

Table 6. Calculated standard ellipse area (SEA) percent overlap from muscle $\delta^{13}C$ and $\delta^{15}N$ values for all seasons, spring, summer and fall.

Season and Predator	Dolphinfish	Wahoo	Yellowfin Tuna
All year			
Blackfin Tuna	0.6849	0.2677	0.3275
Dolphinfish		1	0.9916
Wahoo			0.5529
Spring			
Blackfin Tuna	0.4293	0.5541	0.0786
Dolphinfish		0.8709	0.9304
Yellowfin Tuna			0.3117
Summer			
Blackfin Tuna	0.658*	0.900	0.386
Dolphinfish		0.7067	0.9201
Wahoo			1
Fall			
Blackfin Tuna	0.5431	0.4160	0.6190
Dolphinfish		0.7567	0.4791
Wahoo			0.3811

DISCUSSION

This study represents the first quantitative description of the diets, dietary overlap, and seasonal variation in feeding habits among multiple sympatric pelagic fish predators in the U.S. South Atlantic. It also represents the first comprehensive evaluation of the foraging ecology of blackfin tuna in U.S. waters, using both diet and stable isotope analysis. Additionally, the analysis of isotopic niche width and overlap represents a novel approach for using stable isotope data to evaluate potential competitive interactions among fish predators, which can be used to supplement and/or confirm the results of dietary overlap indices.

Stomach contents and prey importance—Blackfin tuna, dolphinfish, wahoo and yellowfin tuna consumed a high diversity of prey that included 123 different taxa from 62 orders and families identified from their diets throughout all seasons. The high diversity of prey in the diets of these predators suggest that they are generalist predators within the pelagic environment of the U.S. South Atlantic. Seventeen orders and families dominated the diets of the predators by mass (%MM > 1) and occurrence (%FO > 1) with 14 of these occurring in at least three of the predators. The dominant prey comprised four broad groupings based on their habitat and size: (1) prey associated with floating *Sargassum* and other floating debris, which included fish from the families Balistidae, Monacanthidae, Diodontidae, Tetraodontidae, juvenile Carangids, and invertebrates of the order Decapoda which mostly consisted of swimming crabs (Portunidae) and prawns (Aristeidae and Sicyoniidae); (2) surface-schooling prey not typically associated with floating structure, which mainly consisted of fish from the family Exocoetidae; (3) schooling fish and molluscs that can be found in surface waters but mostly occur deeper, which included fish of the families Scombridae, Dussumieriidae and large Carangids, and cephalopods of the families

Loliginidae, Ommastrephidae and Argonautidae; and (4) small schooling crustaceans in the orders Stomatopoda, Amphipoda and Isopoda.

Blackfin tuna had the least piscivorous diet among the predators, with crustaceans and cephalopods and other molluscs accounting for over half the mass and number of prey recovered. Small crustaceans in the orders Amphipoda, Isopoda and Stomatopoda were most common and were found in the diets of fish of all sizes (Figure 2a), suggesting that blackfin tuna may use their gill rakers to retain small invertebrate prey during ram feeding on prey aggregations. Cephalopods of the family Argonautidae, Loliginidae and Ommastrephidae also occurred in the diets of blackfin tuna of all sizes and were the largest prey consumed by fish < 60 cm FL (Figure 2a). Fish of the families Scombridae, Exocoetidae and Stromateidae were the most common fish prey recovered from the diets of fish > 60 cm FL and accounted for the most dietary mass of the larger fish. Headley et al. (2009) observed a similar diet shift in blackfin tuna from Tobago, where smaller individuals mainly consumed crustaceans and juvenile fishes, with an ontogenetic shift to a diet dominated by squid and epipelagic fishes. Interestingly, both epipelagic and mesopelagic fish species were identified in the diets of blackfin tuna, indicating that they either feed in deep water during the day time or that feeding may occur at night when mesopelagic prey migrate into surface waters. Taquet et al. (2000) reported the capture of blackfin tuna on daytime oblique longline sets to a depth of 130m which supports the hypothesis that blackfin tuna most likely feed on mesopelagic prey as they migrates towards the surface overnight. To the best of our knowledge, no tagging studies of blackfin tuna have been conducted to date so diving behavior is unknown.

Dolphinfish had very diverse diets and were mostly piscivorous in their prey selection which was dominated by *Sargassum* associated species and surface schooling prey. Other studies investigating the foraging ecology of dolphinfish have also found that prey associated

with floating structure were of high importance (Manooch et al. 1984; Oxenford and Hunte 1999; Rose and Hassler 1974; Rudershausen et al. 2010; Tripp-Valdez et al. 2010). Dominant prey recovered from the diets of dolphinfish based on frequency of occurrence and mass included juvenile carangids, porcupine fish, filefish, pufferfish and sargassum swimming crabs, which have been found to show high fidelity for *Sargassum* spp. habitat in the Gulf Stream waters of the Northwest Atlantic (Casazza and Ross 2008; Coston-Clements and Center 1991). The high occurrence of *Sargassum* and other floating debris in their stomachs, as well as prey known to associate with *Sargassum*, highlights the importance of floating structure as a pelagic foraging habitat for dolphinfish. Other important prey species recovered that are not generally associated with *Sargassum* included flying fish, jacks, bullet tuna (*Auxis* spp.), paper nautiluses and shortfin squid (*Illex* illecebrosus), as well as cannibalized dolphinfish. A wedge-shaped distribution of predator and prey sizes was observed for dolphinfish and is consistent with other studies reporting increases in maximum prey size for larger dolphinfish (Rudershausen et al. 2010). Larger dolphinfish still consumed small prey items with minimum and median prey sizes increasing very little with predator length (Figure 2b; Table 2). Farrell et al. (2014) observed that dolphinfish harvested near or within mats of floating *Sargassum* were smaller than fish harvested away from the floating mats. As dolphinfish increase in size, they may realize increases in swimming speeds that enable them to pursue larger, faster swimming schooling prey away from the *Sargassum*.

The feeding habits of wahoo demonstrated relatively low prey diversity compared to the diets of the other predators in the study. Wahoo diets were dominated by surface and deep schooling prey which is consistent with other studies in the Atlantic that have observed large squid and scombids as the primary prey of wahoo (Manooch and Hogarth 1983; Rudershausen et al. 2010; Vaske et al. 2003). The most dominant prey by occurrence, mass and number in the

diets of wahoo was bullet tuna, which occurred in more stomachs and accounted for more prey mass than any other individual prey item for any predator included in the study which suggests that wahoo may specialize on bullet tuna in the South Atlantic Bight. Other important fish prey included flying fish, large jacks, file fish and trigger fish, but these fish occurred with low frequency relative to scombids. Paper nautiluses, shortfin squid, longfin inshore squid and Atlantic bird squid were the most dominant squid and octopods found in wahoo diets and were more commonly eaten during the spring and summer. Crustaceans were noticeably absent from the diets of wahoo with the exception of three stomachs that contained unidentifiable decapod remains or crab zoea. These crustacean remains were most likely consumed by other prey that were eaten by the wahoo because of the simultaneous occurrence of heavily digested fish remains in the stomachs. Manooch and Hogarth (1983) also noted the absence of crustaceans and small prey items in the diets of wahoo in this region and attributed it to the lack of gill rakers in this species. Prey sizes in wahoo diets were larger on average than prey sizes consumed by other predators. Wahoo were also the largest predator, other than blue marlin, sampled for diets and their greater size may allow them to swim faster and pursue larger and faster prey than the other predators in the community.

Yellowfin tuna diets were similar to blackfin tuna with a high occurrence of crustaceans and cephalopods. Schooling fishes however, were the most dominant prey of yellowfin by mass, abundance and occurrence and were comparable in their dietary composition to wahoo. Similar foraging ecology was also observed for yellowfin tuna from the eastern and western Pacific (Allain 2005) and the western Indian ocean (Potier et al. 2007). Amphipods were the most dominant crustacean prey recovered and occurred in fish of all sizes suggesting that, like blackfin, yellowfin may use their gill rakers to strain food as they swim through prey aggregations. Yellowfin tuna was the most teuthophagous predator sampled based on mass with

shortfin squid (*Illex illecebrosus*) being the most dominant cephalopod prey recovered from their diets. Bullet tuna and flying fish were the most dominant fish prey in their diets but *Sargassum* associated species were also common in the diets, especially for smaller yellowfin tuna. As yellowfin grow and become more endothermic, they undergo ontogenetic shifts in habitat and diet by expanding their depth range and feeding less on epipelagic prey (Carey and Olson 1982; Graham 2007a; Schaefer et al. 2007; Vaske et al. 2003; Weng et al. 2009). Minimum and median prey sizes recovered from the diets of yellowfin tuna increased at moderate rates when compared to the other predators (Figure 2d; Table 2), but maximum prey sizes did not change significantly over the size range sampled. Graham et al. (2007a) observed a dietary shift by yellowfin tuna in the central Pacific at around 45 - 50 cm FL, from mostly larval crustaceans to fishes and larger invertebrates. Except for one 46.6 cm FL individual, all yellowfin tuna sampled during this study ranged from 63.6 – 140.7 cm FL and were already consuming large fish prey (Figure 2d). Therefore, the range of yellowfin tuna sizes sampled during this study may have been too narrow to reveal any ontogenetic diet shift for the species.

Stable isotope analysis and community structure—There was a high degree of overlap among the predators in the study in both muscle and liver stable isotope values and the isotopically derived estimates of trophic position (TP). However, differences among species were still evident and trophic groupings based on stable isotope values provided a conceptual framework for describing and evaluating the predator-prey community of the U.S. South Atlantic pelagic ecosystem. Two tissue types were used to describe the community based on the premise that isotopic ratios within the tissues of a consumer are a function of the metabolic turnover of that particular tissue; thus allowing for the characterization of foraging habitat and trophic position over different temporal scales (Fry 2006; Hobson 1999; Menard et al. 2007). Liver and muscle tissue in fish have

different turnover rates and can be used to identify dietary shifts on the order of weeks or months, respectively, which can provide information on diet switching across seasonal time scales (Buchheister and Latour 2010; Logan et al. 2006; MacNeil et al. 2005; MacNeil et al. 2006).

The mean TP for all predators sampled during the study ranged from 3.5 to 5.3 and from 4.6 to 5.9 based on $\delta^{15}N$ values in muscle and liver tissue, respectively (Table 4). Dolphinfish, yellowfin tuna, king mackerel, skipjack tuna and rainbow runner all occupied the lowest TP among predators with blue marlin, blackfin tuna and wahoo occupying an intermediate TP, and little tunny, big eye tuna and shortfin mako occupying the apex trophic position (Figure 10). Most prey species recovered from the diets occupied trophic positions that were 1 -2 trophic levels below the predators (Table 5) and grouped together separately from the predators into two distinct groups: (1) *Sargassum* associated species and (2) larger schooling species that also included conspecific prey of dolphinfish and yellowfin tuna (Figure 11). Shortfin squid was the only prey species that grouped with the predators and had an estimated mean TP (3.9) equivalent to the intermediate predator trophic level (Table 5; Figure 11). Predators in the lowest TP had similar diets which consisted mainly of small invertebrates, epipelagic schooling fishes, and fishes associated with *Sargassum* habitat. These predators also had the lowest mean $\delta^{15}N$ and $\delta^{13}C$ values among the predators examined. Dolphinfish and yellowfin tuna diets were similar in that they both fed on small, epipelagic fishes such as round herring, small jacks, filefish, pufferfish, and schooling fishes like flying fish that all had TP's ranging from 1.7 – 2.7 (Table 5). However, yellowfin tuna also fed extensively on prey at higher trophic levels such as shortfin squid and bullet tuna, which occupied TP's similar to their own. However, this was not reflected in yellowfin tuna TP estimates. Logan and Lutcavage (2012) also observed that dolphinfish and yellowfin tuna from the North Atlantic had similar $\delta^{15}N$ and $\delta^{13}C$ values and occupied a similar

trophic level. A possible reason for the discrepancy between yellowfin tuna TP and their diet could be that the tuna sampled may have recently migrated to the area and had not yet achieved isotopic steady state with the local food web. If the tuna were previously in an area that had lower stable isotope baseline values, but similar foraging ecology, then individuals moving into a new area and feeding on the same prey guilds would show a $\delta^{15}N$ value that was lower than the TP they were feeding on in the South Atlantic Bight.

Blackfin tuna and wahoo shared a similar TP based on both muscle and liver stable isotope values but their diets were not similar. Bullet tuna, the dominant prey in wahoo diets, had a mean TP value ~1 trophic level below wahoo. Blackfin tuna mostly consumed crustaceans and squid which had relatively high mean TP values (3.3 for *Sargassum* swimming crabs and 3.9 for shortfin squid) (Table 5). Therefore, even though wahoo and blackfin diets differed, they fed on prey types that occupied similar trophic levels which contributed to their comparable $\delta^{15}N$ values and TP. Blue marlin also occupied the same TP as blackfin tuna and wahoo based on $\delta^{15}N$ and $\delta^{13}C$ values. Rudershausen et al. (2010) observed that blue marlin and wahoo in the North Atlantic had very similar diets and that both species relied heavily upon bullet tuna. Indeed, of the nine blue marlin sampled during this study that had prey in their stomachs, seven of them contained bullet tuna. The other two diets that had measurable prey contained skipjack tuna and dolphinfish which had estimated TP's of 3.3 and 3.0, respectively (Table 5).

Shortfin mako, bigeye tuna and little tunny occupied the highest trophic level within the community and were each estimated to be one TP higher than the other predators (Table 4). Foraging ecology studies for shortfin mako in the North Atlantic have identified Ommastrephidae squid, scombrids (*Scomber* spp.; *Thunnus* spp,) and swordfish (*Xiphias gladius*) as important prey (Maia et al. 2006; Stillwell and Kohler 1982). Revill et al. (2009) observed shortfin mako to occupy a trophic level above large tuna and billfish in the Western

Pacific. Bigeye tuna are known to forage throughout wide depth ranges (Dagorn et al. 2000), consume large squid (Potier et al. 2004), and occupy trophic levels similar to swordfish and other large tunas (Polovina et al. 2009; Young et al. 2010). Interestingly, mean $\delta^{15}N$ values for little tunny were the highest for any species measured during this study. Little tunny foraging ecology is believed to be similar to other small coastal tuna species (Falautano et al. 2007; Manooch et al. 1985), and functionally they are not found to occupy apex trophic levels within food webs. Cai et al. (2007) also observed high $\delta^{15}N$ values in little tunny muscle from the Gulf of Mexico, with the values being higher than those observed for blue marlin and wahoo, which feed on larger prey.

A variety of factors can affect the accuracy of TP estimates derived from stable isotope data, requiring careful examination when interpreting the results. To obtain accurate estimates, four assumptions must be met: (1) the organisms being measured must have reached an isotopic equilibrium with the local food web, (2) all species within the food web must have consistent trophic discrimination factors, (3) the organism must occupy the environment during the time period necessary for total tissue turnover, and (4) the isotopic baseline values of the system must remain constant throughout the time period investigated (Post 2002). Depending on the tissue type being used, isotopic turnover can take weeks (liver) to several months (muscle), during which the fish can migrate and feed in multiple areas with varying isotopic baselines that can confound the estimates of trophic level. Also, the trophic enrichment factors for the predators studied are poorly understood and most likely vary among species, tissue types, and diet (Buchheister and Latour 2010; Pinnegar and Polunin 1999; Sweeting et al. 2007). Care must be taken when choosing trophic enrichment factors since estimates of TP are especially sensitive to this value (Post 2002). Enrichment factors of 2.3‰ for muscle tissue and 1.3‰ for liver tissue that were generated during experiments with yellowfin tuna were applied during this study

because of the similarity with the other predator species (Graham 2007b). Mean $\delta^{15}N$ and $\delta^{13}C$ values of predators were more enriched than their prey and, assuming an enrichment factor of 2.3‰, five trophic levels were present in the nearshore pelagic community off the southeast U.S. coast. However, there was a high degree of trophic overlap among the predators due to their omnivorous feeding strategies, which can cause TP estimates of upper trophic level fish to be less distinct between levels (Post 2002).

The trophic level of a piscivorous fish is generally thought to increase with increasing predator size because of ontogenetic expansion of the feeding niche related to increases in mouth gape and swimming speed (Juanes et al. 2002; Scharf et al. 2000). Ratios of nitrogen isotopes exhibit stepwise increases with each trophic level and are expected to increase with body size among fishes (Jennings et al. 2001; Jennings et al. 2002). Stable isotope values of nitrogen from muscle generally increased with size for blackfin tuna, dolphinfish, and wahoo during this study, indicative of an increase in trophic position with body size. This relationship is consistent with the diet data for these species, which showed an increase in the sizes of prey consumed at larger predator body sizes. There was no relationship detected between yellowfin tuna body size and muscle $\delta^{15}N$ values, which aligns with previous studies from the Indian Ocean (Menard et al. 2007) and North Atlantic (Logan and Lutcavage 2012), and was also consistent with yellowfin diet data where maximum sizes of prey did not change across a range of yellowfin body sizes. However, liver $\delta^{15}N$ values of yellowfin tuna declined at larger body sizes. The lack of a relationship between the muscle $\delta^{15}N$ values and body size combined with the negative size-dependence of liver $\delta^{15}N$ values could also be due to yellowfin tuna recently migrating to the sampling area and not yet reaching isotopic equilibrium with the local food web. Muscle $\delta^{13}C$ values increased at larger body sizes for blackfin tuna and dolphinfish, which was consistent with the observed dietary changes for the two species. $\delta^{13}C$ values are typically useful for

differentiating between foraging habitats and are assumed to increase very little with trophic level (DeNiro and Epstein 1976), whereas $\delta^{15}N$ values generally increase ~2.3‰ per trophic level (Graham 2007b). Blackfin tuna and dolphinfish $\delta^{15}N$ values in muscle tissue had a range of 6.1‰ and 5.0‰ respectively, representing an increase in TP of about 2.5 levels that could partially explain the observed ontogenetic increase in carbon isotopes.

Seasonal trends in diet and trophic position—Seasonal variability in mass, abundance, frequency of occurrence, as well as muscle and liver stable isotopes was observed in the diets of each of the predators. Except for blackfin tuna, samples sizes were only sufficient to characterize the diets of the predators during the spring, summer and fall seasons. Blackfin tuna demonstrated the most variation in diet across the seasons with summer, fall and winter diets dominated by crustaceans. *Sargassum* associated species did occur more frequently in the summer diets, while the frequency and mass of bullet tuna increased in the fall. Spring diets were dominated by flying fish, but crustaceans were still frequent in the diets. $\delta^{13}C$ values in liver tissue were enriched in the summer, which could have been related to a shift in the foraging behavior and habitat use of blackfin tuna during this time. Big eye tuna had similar $\delta^{13}C$ values to blackfin tuna in muscle tissue across seasons. Big eye are known to forage at deeper depths than the other predators in the study and also feed heavily on cephalopods and octopods (Young et al. 2010). Blue marlin are most abundant in the area during the summer and have been shown to feed on blackfin tuna and other small tuna species (Rudershausen et al. 2010; Veiga et al. 2011). Thus, blackfin tuna may be actively avoiding predation by foraging at deeper depths than blue marlin during summer. Dolphinfish diets did not vary considerably among seasons but slight differences in the frequency of occurrence and contribution by mass of flying fish and *Sargassum* associated prey did occur. Flying fish were most dominant in the diets during spring

and then declined in throughout the summer and fall. Filefish, small jacks and porcupinefish increased in occurrence during summer and dominated the diets during the fall. *Sargassum* algae is an ephemeral habitat and is usually at its highest abundance during summer and early fall (Coston-Clements and Center 1991; Rooker et al. 2006). During spring, when it is not as abundant, dolphinfish may be foraging more on open water prey and then switch to *Sargassum* associated species when they occur in higher densities in the environment. Wahoo had the most consistent diet of any predator across seasons. Bullet tuna were the dominant prey for every season, while paper nautiluses contributed to the diet in the spring, shortfin and longfin squid, porcupine fish and flying fish were important during summer, and jacks and flying fish in the fall. A seasonal difference in liver $\delta^{15}N$ values was observed with wahoo from the spring and fall having higher $\delta^{15}N$ values than fish from the summer. The lower TP of wahoo during summer may be due to a greater contribution of low trophic level prey to the diet, such as porcupine fish and flying fish, and could mean that wahoo are taking advantage of seasonally abundant prey. Yellowfin tuna diets varied among seasons with fish prey dominating during spring and fall, and crustaceans and fish dominating the diets during summer. Bullet tuna was the most important prey to yellowfin in the spring, contributing to almost half the dietary mass. Summer yellowfin diets were more diverse with crustaceans, shortfin squid and bullet tuna all contributing substantially to dietary mass, while flying fish, bullet tuna and shortfin squid were primary prey in the fall. Seasonal differences in liver $\delta^{15}N$ values were also observed for yellowfin tuna with fish from the fall having the highest $\delta^{15}N$ and TP.

Interspecific competition—Among blackfin tuna, dolphinfish, wahoo and yellowfin tuna caught in the South Atlantic Bight, dietary overlap was highest between pairs of predators that consumed either mostly *Sargassum* associated prey (dolphinfish and blackfin tuna) or large

schooling fishes and cephalopod prey (yellowfin tuna and wahoo). Seasonally, these relationships were most pronounced in the spring, especially between yellowfin tuna and wahoo which had almost complete overlap ($\alpha = 0.9439$) during this period. For both predators, scombrid fishes constituted > 40% of dietary mass during spring, which likely contributed most to the high levels of diet overlap. Blackfin tuna and dolphinfish also exhibited high dietary overlap in the spring, which was attributed to the contributions of flying fish and crustaceans to the diets of both predators. Wahoo and yellowfin tuna were the only species to show significant overlap during the summer, but it was less than that observed during spring. Scombrid fishes and squid were the dominant prey in the diets of the two species during summer. Significant dietary overlap between wahoo and yellowfin tuna has also been observed in the equatorial Atlantic (Vaske et al. 2003) and along the U.S. Southeastern Atlantic Coast (Rudershausen et al. 2010), with both studies identifying schooling fishes and ommastrephid squid as the dominant prey contributing to the overlap. Additionally, Rudershausen et al. (2010) only sampled fish from a single, annual fishing tournament that occurred in early summer and observed similar values of overlap ($\alpha = 0.591$) to those observed in this study ($\alpha = 0.647$).

The use of stable isotopes to estimate the isotopic niche width of a predator draws from the ideas of G. E. Hutchinson in that ecological niches can be represented as a hypervolume in infinite dimensional space with axes that represent ecological variables (Jackson et al. 2011). Stable isotopes can be used to characterize the niche of a predator because the variation in the assimilation of stable isotopes into the tissue of an individual is related to its diet and allows for individual variation in feeding to be accounted for at the population level (Newsome et al. 2007). Isotopic bi-lots of carbon and nitrogen account for the trophic level of an individual ($\delta^{15}N$) and foraging habitat ($\delta^{13}C$) and can be used to estimate a community level niche space that can then be compared with other species that occupy the same ecosystem. Blackfin tuna, dolphinfish,

wahoo, and yellowfin tuna all had similar niche diversities indicated by the high total area of the convex polygons and their overlaps within isotopic space. The large isotopic niches of these predators are supported by the diet data which indicated a high degree of omnivory among the predators with a high diversity of prey found in their diets. The niche widths of the predators, measured as standard ellipse area, varied among species, with dolphinfish having niche widths that encompassed over twice the isotopic area of the other predators. Diet data revealed that dolphinfish expanded their feeding niche more than any other species by incorporating larger schooling prey into their diets while still consuming smaller, *Sargassum* associated prey. The degree of isotopic niche overlap among the species was similar to the dietary overlaps estimated from the prey mass data. The measure of niche overlap (0.6849) between blackfin tuna and dolphinfish was similar to the Schoener's index estimated from the diet data ($\alpha = 0.6491$) and is evidenced by the overlap of the two ellipses (Figure 12). Dolphinfish niche widths overlapped considerably with wahoo and yellowfin tuna even though no significant overlap of these species was observed using Schoener's index estimated from the diet data. This is most likely due to the large isotopic niche diversity of dolphinfish and the broad niche width of the standard ellipses encompassing both the ellipses of wahoo and yellowfin tuna.

Conclusions—This study provides valuable insight into the community structure and foraging ecology of large pelagic fishes in the U.S. South Atlantic and provides baseline data for future studies of ecosystem function. A few caveats to note were that sampling of predator diets and tissues was limited to fishing tournaments and charter operations, and undoubtedly biased sample collection towards larger fish and limited the ability to evaluate ontogenetic relationships across all possible sizes of predators (e.g. juvenile). The study is novel in that it provides seasonal diet information and assesses the potential for competition among multiple sympatric

predators in the U.S. South Atlantic using both diet analysis and stable isotope techniques. In this sense, it represents the most comprehensive study of trophic ecology in this pelagic ecosystem to date.

Despite evidence for generalist foraging behaviors and the high diversity of prey found in the diets of most of the predators sampled, a few fish and invertebrate species contributed disproportionally more to the diets of the predators indicating they may be key forage base in pelagic habitats. Bullet tuna were important in the diets of wahoo and yellowfin tuna during all seasons, contributing to the high dietary overlap between the two species, and are also believed to be of high dietary importance to other predators within the region (e.g., blue marlin; Rudershausen et al. 2010). However, there is sparse published information on the biology and population dynamics of these important prey species in the Western Atlantic (Carpenter 2002), necessitating the need for research on bullet tuna before ecosystem-based management of these fisheries can be implemented. Additionally, ommastrephid squid, particularly *I. illecebrosus* were found to be important prey for most of the predators studied but very little is known about their diversity and abundance in the region (Staudinger et al. 2013). By instituting long-term monitoring programs of predator diets and tissue sampling and fisheries independent sampling of the predator and prey communities within this region of the Northwest Atlantic, ecosystem level changes within the community can be monitored to inform fisheries management within the region.

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Table A. Stomach contents by percent frequency of occurrence (%O), mean percent mass ($\overline{\%M}$), and mean percent number ($\overline{\%N}$) of blackfin tuna, dolphinfish, wahoo, and yellowfin tuna collected from April 2010 to October 2013.

	Blackfin Tuna			Dolphinfish			Wahoo			Yellowfin Tuna		
Prey Taxon	**%O**	$\overline{\%M}$	$\overline{\%N}$	**%O**	$\overline{\%M}$	$\overline{\%N}$	**%O**	$\overline{\%M}$	$\overline{\%N}$	**%O**	$\overline{\%M}$	$\overline{\%N}$
Crustaceans	73.41	46.45	42.93	24.47	10.57	11.77	1.41	Trace	0.37	43.92	21.74	26.31
Amphipoda	15.36	4.36	3.89							43.92	10.59	9.70
Hyperiidae	1.50	0.46	0.33									
Hyperia spp.	1.50	0.46	0.33									
Decapoda	46.44	21.56	20.39	21.84	9.93	10.29	0.70	Trace	0.16	28.57	8.47	11.70
Aristeidae	1.87	0.33	0.31	0.26	0.01	0.08				5.29	1.81	1.73
Plesiopenaeus armatus	1.87	0.33	0.31	0.26	0.01	0.08				4.23	1.78	1.48
Pandalidae	0.37	0.08	0.08	0.26	0.18	0.08						
Pandalus spp.	0.37	0.08	0.08	0.26	0.18	0.08						
Portunidae	2.62	0.88	0.90	16.84	8.26	7.62				5.82	0.54	1.40
Arenaeus cribarius				0.26	0.07	0.08						
Callinectes spp.										0.53	0.17	0.13
Ovalipes ocellatus				0.26	0.26	0.25						
Ovalipes stephensoni	0.37	0.13	0.19									
Portunus sayi	2.25	0.75	0.72	13.42	6.41	6.24				3.70	0.34	0.93
Portunus spinicarpus				0.26	0.20	0.12						
Scyllaridae	0..37	0.13	0.19							0.53	0.55	0.50
Sicyoniidae	1.12	0.33	0.36	1.32	0.18	0.39						
Euphausiacea	2.62	0.59	0.51									
Isopoda	15.73	4.60	3.91	0.26	0.26	0.21				0.53	0.22	0.20
Stomatopoda	27.34	9.52	9.36	0.53	0.07	0.19				2.12	0.66	0.89
Unidentified crustaceans	21.35	5.82	4.86	2.63	0.32	1.08	0.70	Trace	0.16	5.29	1.80	3.81
Fish	73.78	33.88	32.04	89.74	81.80	77.04	95.07	92.67	83.54	78.31	62.18	53.52
Anguilliformes	0.37	0.04	0.04	0.53	0.07	0.10						
Nemichthyidae	0.37	0.04	0.04	0.53	0.07	0.10						
Labichthys carinatus				0.26	0.07	0.06						

Atheriniformes				1.05	0.65	0.60						
Atherinopsidae				1.05	0.65	0.60						
Menidia menidia				1.05	0.65	0.60						
Beloniformes	12.73	8.47	8.01	23.42	19.70	13.39	5.63	4.16	3.46	4.76	4.07	3.25
Belonidae	0.75	0.21	0.18							0.53	0.20	0.17
Tylosurus crocodilus	0.37	0.13	0.13									
Exocoetidae	11.61	7.98	7.55	22.89	19.18	12.84	4.23	2.96	2.62	3.70	3.33	2.58
Cypselurus spp.				0.26	0.24	0.06						
Exocoetus obtusirostris				0.26	0.26	0.12						
Hemiramphidae				0.53	0.53	0.50	1.41	1.20	0.84	0.53	0.55	0.50
Hemiramphus brasiliensis				0.53	0.53	0.50	1.41	1.20	0.84	0.53	0.55	0.50
Scomberesocidae	0.75	0.29	0.28	0.26	Trace	0.05						
Scomberesox saurus	0.75	0.29	0.28	0.26	Trace	0.05						
Clupeiformes	3.00	1.02	1.00	2.37	1.73	1.65	1.41	0.71	0.47	1.59	1.36	0.75
Clupeidae	1.87	0.54	0.53				0.70	0.06	0.16			
Alosa aestivalis	0.37	0.04	0.03									
Clupea harengus	0.75	0.25	0.24									
Dussumieriidae	1.12	0.48	0.47	2.37	1.73	1.65	0.70	0.66	0.31	1.59	1.36	0.75
Etrumeus teres	1.12	0.48	0.47	2.37	1.73	1.65	0.70	0.66	0.31	1.59	1.36	0.75
Gadiformes	0.37	0.10	0.09									
Phycidae	0.37	0.10	0.09									
Urophycis spp.	0.37	0.10	0.09									
Lophiiformes				0.53	0.53	0.37						
Antennariidae				0.53	0.53	0.37						
Histrio histrio				0.53	0.53	0.37						
Mugiliformes				0.26	0.22	0.12	0.70	0.70	0.31			
Mugilidae				0.26	0.22	0.12	0.70	0.70	0.31			
Myctophiformes	1.12	0.18	0.18	0.26	0.05	0.12	0.70	Trace	0.21			
Myctophidae	1.12	0.18	0.18	0.26	0.05	0.12	0.70	Trace	0.21			
Diaphus spp.				0.26	0.05	0.12	0.70	Trace	0.21			
Myctophum selenops	0.37	0.04	0.04									

Ophidiiformes				0.26	0.06	0.12						
Ophidiidae				0.26	0.06	0.12						
Lepophidium cervinum				0.26	0.06	0.12						
Perciformes	17.60	8.00	7.74	27.89	16.65	14.94	50.00	46.32	32.65	30.69	26.88	21.07
Ariommatidae										0.53	0.55	0.50
Ariomma bondi										0.53	0.55	0.50
Bramidae	0.75	0.23	0.41	0.26	0.03	0.04	0.70	0.70	0.63	1.59	0.70	0.70
Brama brama							0.70	0.70	0.63			
Pterycombus brama										1.06	0.69	0.60
Carangidae	3.75	1.21	1.05	16.84	9.01	8.08	3.52	1.79	1.57	4.76	3.61	2.83
Caranx bartholomaei				1.58	0.62	0.73						
Caranx crysos				0.53	0.18	0.15						
Caranx ruber				0.26	0.01	0.08						
Caranx spp.				2.63	1.07	0.89						
Chloroscombrus chrysurus				1.32	0.83	0.68				0.53	0.55	0.50
Decapterus punctatus				0.26	0.26	0.25						
Decapterus spp.	1.12	0.21	0.08	2.37	1.13	1.21	2.11	1.06	1.05	2.12	1.52	1.17
Hemicaranx amblyrhynchus				0.53	0.29	0.28						
Naucrates ductor				0.26	0.07	0.06						
Selene setapinnis	0.37	0.19	0.19									
Selene spp.				0.26	0.04	0.05						
Selene vomer				1.05	0.53	0.39						
Seriola dumerili				0.53	0.53	0.50						
Seriola spp.				0.26	0.03	0.05						
Seriola zonata				0.79	0.26	0.29						
Trachurus lathami	0.75	0.32	0.31	0.53	0.29	0.13	0.70	0.13	0.21			
Uraspis secunda				0.53	0.31	0.37						
Coryphaenidae				2.89	1.70	1.81						
Coryphaena hippurus				2.89	1.70	1.81						
Echeneidae	1.50	0.60	0.59				0.70	0.59	0.31	0.53	0.09	0.25
Echeneis spp.	0.37	0.10	0.09									

Remora spp.										0.53	0.09	0.25
Gempylidae	0.37	0.13	0.13				0.70	0.28	0.10			
Gempylus serpens							0.70	0.28	0.10			
Istiophoridae				0.26	0.14	0.08						
Priacanthidae										0.53	Trace	Trace
Sciaenidae				0.26	0.17	0.12						
Scombridae	5.99	3.43	3.11	4.21	3.34	2.43	43.66	41.68	28.72	20.63	20.00	14.89
Auxis spp.	3.37	1.74	1.57	2.11	1.98	1.16	23.94	22.88	14.68	12.17	11.97	8.58
Katsuwonus pelamis				0.26	0.13	0.06				0.53	0.19	0.17
Sarda sarda				0.53	0.28	0.28						
Thunnus albacares							0.70	0.70	0.63	0.53	0.54	0.25
Serranidae	.75	0.21	0.21	1.05	0.37	0.31	1.41	0.53	0.52	1.59	0.66	0.83
Centropristis spp.				0.26	0.17	0.08						
Epinephelus spp.	0.37	0.04	0.04									
Mycteroperca spp.				0.26	0.09	0.12				0.53	0.01	0.25
Synagrops spp.							0.70	0.35	0.31			
Sphyraenidae	0.37	0.13	0.09							0.53	0.31	0.17
Sphyraena spp.	0.37	0.13	0.09							0.53	0.31	0.17
Stromateidae	5.24	1.85	1.81	3.42	1.45	1.66	0.70	0.70	0.63	1.59	0.20	0.35
Hyperoglyphe spp.	0.75	0.48	0.47	0.53	0.43	0.33						
Peprilus alepidotus										0.53	Trace	0.10
Peprilus burti	0.37	0.19	0.19	0.53	0.04	0.21						
Peprilus paru	0.37	0.19	0.19	0.79	0.29	0.33				0.53	0.02	0.08
Peprilus spp.	1.87	0.37	0.37	0.26	0.06	0.12						
Peprilus triacanthus	1.50	0.42	0.41	0.53	0.27	0.28	0.70	0.70	0.63	0.53	0.17	0.17
Psenes spp.				0.26	0.09	0.08						
Trichiuridae	1.12	0.21	0.34	1.05	0.33	0.28	0.70	0.04	0.16	1.59	0.75	0.54
Trichiurus lepturus										0.53	0.03	0.08
Xiphiidae				0.26	0.10	0.12						
Xiphias gladius				0.26	0.10	0.12						
Scorpaeniformes	0..7	0.10	0.09	0.26	0.01	0.04	0.70	0.16	0.21	0.53	0.01	0.17

Dactylopteridae				0.26	0.01	0.04	0.70	0.16	0.21	0.53	0.01	0.17
Dactylopterus volitans				0.26	0.01	0.04	0.70	0.16	0.21	0.53	0.01	0.17
Triglidae	0.37	0.10	0.09									
Stomiiformes	0.75	0.07	0.07									
Sternoptychidae	0.75	0.07	0.07									
Sygnathformes	4.12	0.71	0.79	1.58	0.60	0.77				2.12	0.41	0.64
Centriscidae	1.12	0.11	0.11									
Macroramphosus gracilis	0.37	0.04	0.04									
Macroramphosus scolopax	0.37	0.03	0.03									
Macroramphosus spp.	0.37	0.04	0.03									
Syngnathidae	3.75	0.61	0.69	1.58	0.60	0.77				2.12	0.41	0.64
Hippocampus erectus	1.12	0.20	0.20	0.26	0.02	0.12				1.06	0.13	0.29
Hippocampus reidi	0.37	0.08	0.08									
Hippocampus spp.	1.50	0.17	0.21	0.79	0.31	0.46				0.53	0.07	0.10
Tetraodontiformes	7.49	1.69	1.59	31.05	16.03	15.69	9.86	6.56	6.29	10.05	4.07	3.75
Balistidae	0.75	0.08	0.08	3.68	1.43	1.33	1.41	0.85	0.73	1.06	0.27	0.25
Balistes capriscus				0.53	0.15	0.15	0.70	0.70	0.63			
Balistes spp.	0.37	0.04	0.04									
Canthidermis sufflamen				0.26	0.26	0.12	0.70	0.15	0.10			
Diodontidae				10.26	4.51	4.50	4.23	2.13	2.62	1.59	0.30	0.42
Chilomycterus antennatus				0.26	0.12	0.05						
Chilomycterus reticulatus							0.70	0.70	0.63			
Chilomycterus spp.				0.53	0.30	0.19						
Diodon eydouxii				0.26	0.04	0.04						
Diodon holocanthus				5.26	2.48	1.89						
Diodon hystrix				0.26	0.20	0.04						
Diodon spp.				3.42	1.04	1.64	1.41	0.72	0.73	1.59	0.30	0.42
Monacanthidae	4.87	1.14	0.99	20.00	8.83	8.52	2.82	1.81	1.36	6.88	2.60	2.06
Aluterus heudelotii				0.53	0.10	0.08						
Aluterus monoceros				0.53	0.43	0.2				0.53	0.34	0.13
Aluterus scriptus				1.05	0.53	0.32						

Aluterus spp.	0.75	0.23	0.16	3.16	0.97	1.06				0.53	0.27	0.17
Cantherhines pullus				3.68	1.45	1.11						
Cantherhines spp.				0.53	0.10	0.07						
Cantherhines sufflamen				0.26	0.17	0.08						
Monacanthus ciliatus	0.37	0.19	0.13									
Monacanthus spp.	0.75	0.12	0.13	1.84	0.32	0.64	0.70	0.70	0.63	0.53	0.08	0.25
Stephanolepis hispidus	0.37	0.06	0.05	3.95	1.75	1.55						
Stephanolepis setifer				0.79	0.36	0.23						
Stephanolepis spp.				1.32	0.33	0.38						
Tetraodontidae	2.62	0.47	0.52	2.63	1.26	1.34	2.11	1.77	1.57	3.70	0.90	1.02
Canthigaster rostrata				0.26	0.09	0.08						
Lagocephalus spp.	0.75	0.07	0.07	0.53	0.44	0.13	1.41	1.41	1.26	1.06	0.39	0.27
Zeiformes										0.53	0.15	0.07
Zeidae										0.53	0.15	0.07
Zenopsis conchifera										0.53	0.15	0.07
Unidentified fish	49.06	13.50	12.44	45.26	25.49	29.12	45.77	34.05	39.94	44.44	25.23	23.82
Insecta				0.79	0.02	0.31				1.06	0.67	0.33
Odonata				0.26	0.02	0.12						
Mollusks	58.43	19.67	25.03	16.32	7.60	10.88	14.08	7.33	16.09	33.33	15.41	19.84
Cephalopoda	50.19	15.39	20.50	14.21	6.99	9.91	14.08	7.33	16.09	32.28	15.18	19.20
Octopoda	11.99	2.20	3.01	5.79	2.37	3.43	4.23	2.76	3.46	4.23	1.97	4.28
Alloposidae				0.79	0.01	0.19						
Haliphron atlanticus				0.79	0.01	0.19						
Argonautidae	8.24	1.66	2.05	5.00	2.21	3.11	4.23	2.17	3.09	3.17	1.41	3.16
Argonauta spp.	8.24	1.66	2.05	5.00	2.21	3.11	4.23	2.17	3.09	2.65	1.10	2.99
Octopodidae							0.70	0.59	0.21			
Octopus vulgaris							0.70	0.59	0.16			
Teuthida	43.82	11.67	15.93	7.89	4.06	5.69	11.27	4.05	11.84	27.51	13.11	14.63
Ancistrocheiridae				0.26	Trace	0.05						

Ancistrocheirus lesueurii				0.26	Trace	0.05						
Chiroteuthidae							0.70	0.18	0.16			
Chiroteuthis veranyi							0.70	0.18	0.16			
Cranchiidae	0.75	0.11	0.11	0.26	Trace	0.05						
Cranchia Scabra	0.75	0.11	0.11									
Enoploteuthidae	0.75	0.08	0.09							1.59	0.22	0.54
Abralia spp.	0.37	0.05	0.05									
Abralia veranyi	0.37	0.03	0.03							1.06	Trace	0.29
Abraliopsis morisii										0.53	0.22	0.25
Histioteuthidae				0.53	0.26	0.25	0.70	0.18	0.16	0.53	0.55	0.50
Histioteuthis bonnellii				0.53	0.26	0.25	0.70	0.18	0.16			
Lepidoteuthidae	1.50	0.33	0.33									
Lepidoteuthis grimaldii	1.50	0.33	0.33									
Loliginidae	4.87	1.24	1.35	0.53	0.51	0.36	2.82	0.41	1.52			
Doryteuthis pealeii	4.87	1.24	1.35	0.53	0.51	0.36	2.82	0.41	1.52			
Ommastrephidae	16.85	5.25	5.70	4.21	2.70	2.79	5.63	2.22	3.30	19.58	9.78	7.84
Illex illecebrosus	16.48	4.95	5.37	3.16	1.90	2.00	3.52	1.08	2.41	17.99	9.63	7.30
Ornithoteuthis antillarum	1.12	0.15	0.17	0.53	0.27	0.30	2.11	1.14	0.89	1.06	Trace	0.29
Onychoteuthidae	2.25	0.40	0.43	0.26	Trace	0.12						
Onychoteuthis banksii	2.25	0.40	0.43	0.26	Trace	0.12						
Onykia spp.												
Sepiolidae	1.87	0.68	0.67									
Rossia moelleri	1.50	0.29	0.29									
Rossia spp.	0.37	0.39	0.38									
Gastropoda	13.48	4.18	4.43	2.11	0.61	0.97				1.59	0.22	0.64
Aeolidioidae										0.53	0.17	Trace
Glaucidae										0.53	0.17	Trace
Glaucus atlanticus										0.53	0.17	Trace
Cavolinioidae	6.74	2.13	2.33	0.79	0.03	0.25						
Cavoliniidae	6.74	2.13	2.33	0.79	0.03	0.25						
Cavolinia tridentata				0.26	Trace	0.12						

Cavolinia uncinata	0.37	0.10	0.13								
Diacria trispinosa	1.12	0.46	0.45								
Pterotracheoidea	3.00	0.67	0.66	0.53	0.26	0.37			0.53	0.04	0.20
Atlantidae	3.00	0.67	0.66	0.53	0.26	0.37			0.53	0.04	0.20
Unidentified mollusks	0.37	0.10	0.09								
Parasite	13.11			2.63			94.04		18.42		
Trematoda	12.73			2.63			93.62		17.89		
Plagiorchiida	12.73			2.63			93.62		17.89		
Hirudinellidae	12.73			2.63			93.62		17.89		
Hirudinella ventricosa	12.73			2.63			93.62		17.89		
Unclassified	0.37						0.85		0.53		

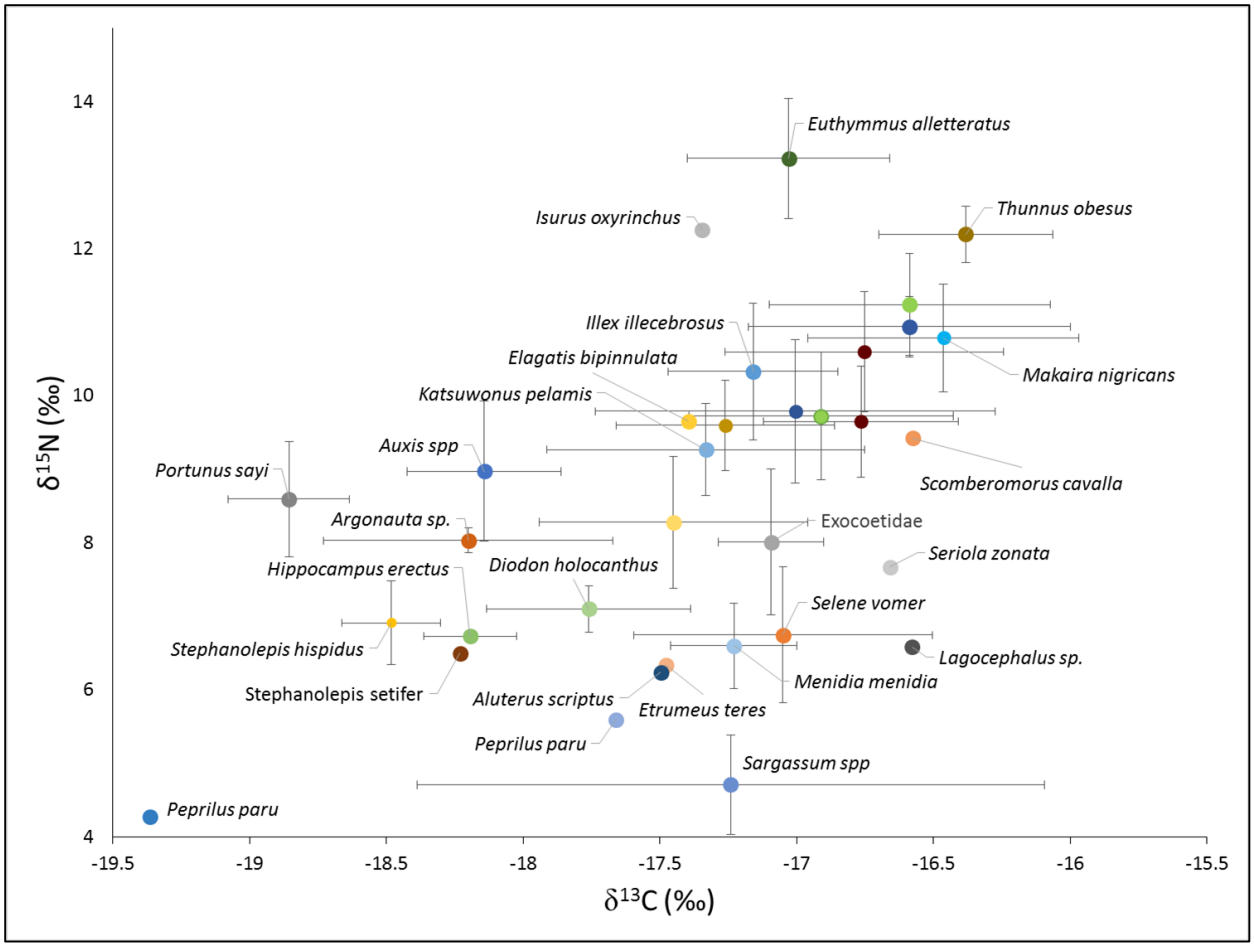

Figure B. Community bi-plot of carbon ($\delta^{13}C$ [‰]) and nitrogen ($\delta^{15}N$ [‰]) ratios in predator (muscle) and prey (muscle or whole body). Each symbol represents mean stable isotopic values with ± 1 standard deviation error bars.

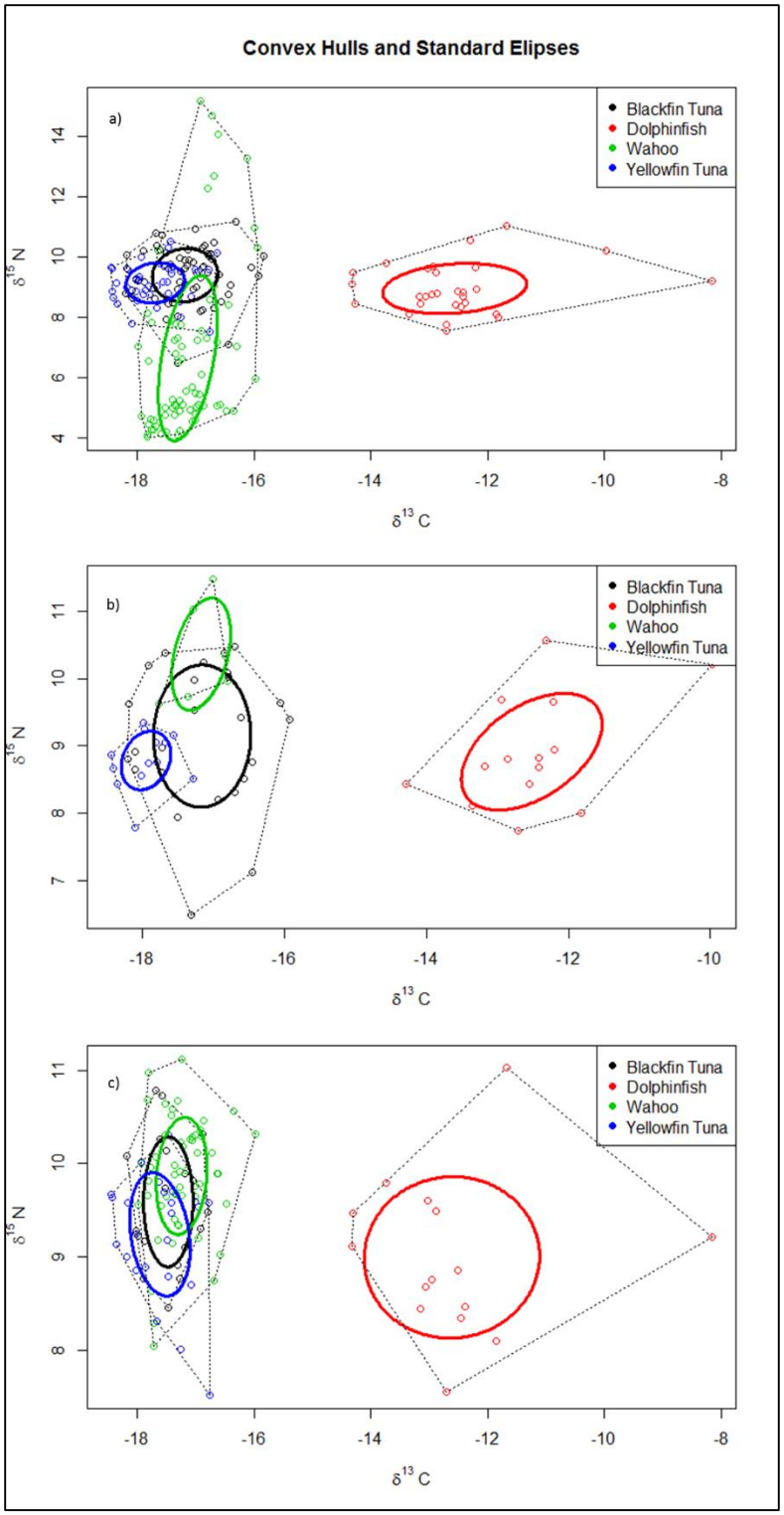

Figure C. Convex hulls (dashed lines) encompassing all data points and standard ellipses (solid lines) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in the liver tissue of blackfin tuna, dolphinfish, wahoo, and yellowfin tuna during the (a) all seasons, (b) spring, and (c) summer.

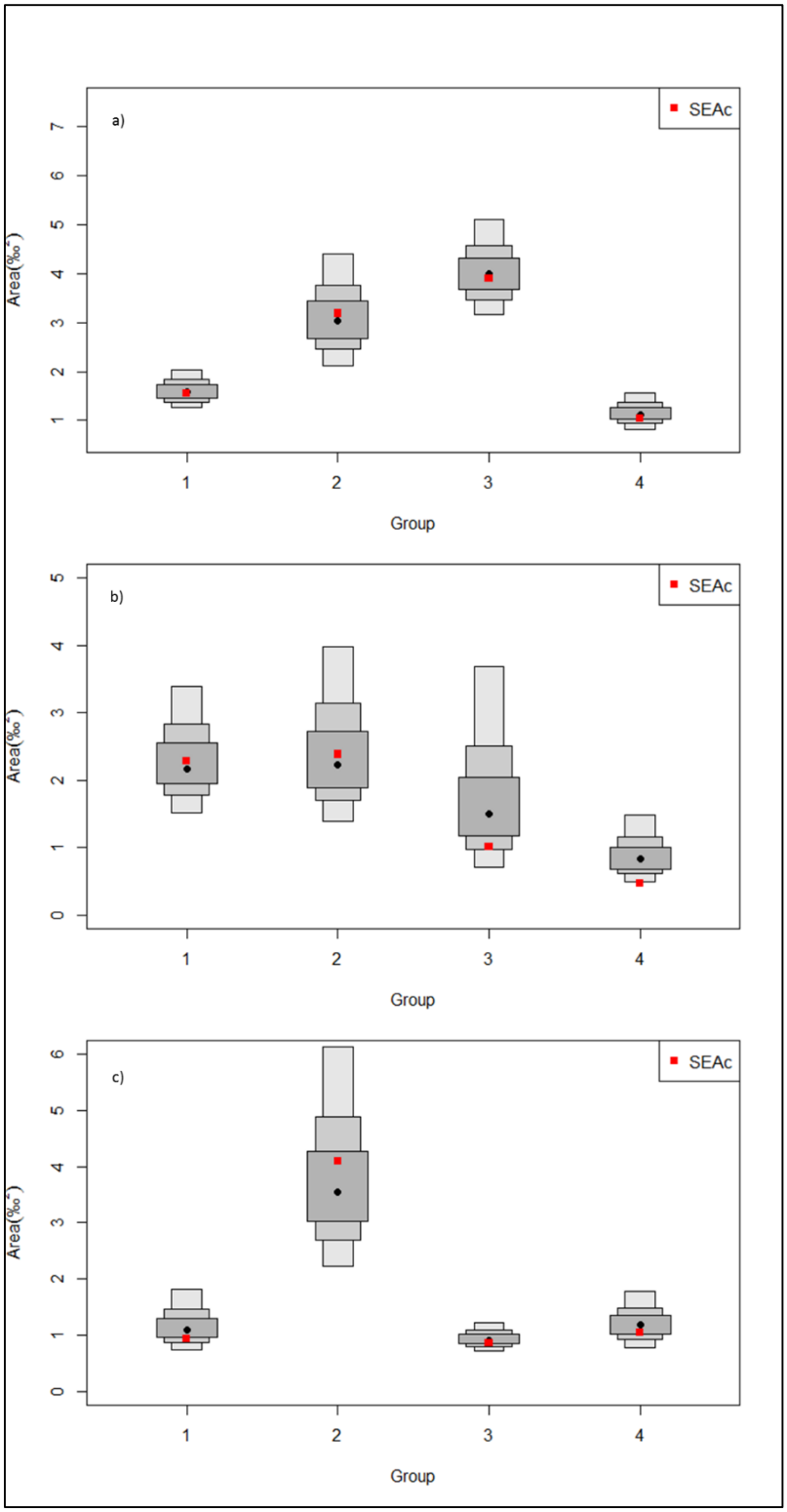

Figure D. Bayesian credible interval estimates of standard ellipse area (SEA) and standard ellipse area estimates corrected for small sample size (SEAc) of (1) blackfin tuna, (2) dolphinfish, (3) wahoo, and (4) yellowfin tuna for (a) all seasons, (b) spring, and (c) summer.