

# Trophic niche overlap among dolphinfish and co-occurring tunas near the northern edge of their range in the western North Atlantic

Amy K. Teffer<sup>1,3</sup> · Michelle D. Staudinger<sup>1,2,4</sup> · Francis Juanes<sup>1,3</sup>

Received: 17 February 2015 / Accepted: 30 July 2015 / Published online: 18 August 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** We present the first quantitative analyses of dolphinfish (*Coryphaena hippurus*) foraging habits and trophic interactions with co-occurring yellowfin (*Thunnus albacares*) and albacore (*T. alalunga*) tunas in the Southern New England region of the western North Atlantic Ocean. Fish caught by recreational anglers in offshore waters of Massachusetts were sampled during the summers of 2007–2010. Diet analysis revealed that shortfin squid (*Illex illecebrosus*) and small pelagic crustaceans were principal prey to dolphinfish, yellowfin tuna, and albacore tuna. A wide variety of *Sargassum*-associated fishes were also important to dolphinfish and yellowfin tuna diets. Dietary (Schoener's index: 0.82–0.86) and isotopic niche (isotopic ellipse overlap: 53.6–64.7 %) overlap was high, and dolphinfish and tunas occupied equivalent trophic positions (TP = 3.4–3.6). Relative prey size in dolphinfish and yellowfin tuna diets exhibited convergence with ontogeny.

Overall, dolphinfish had the greatest isotopic niche width, which was twice as large as yellowfin tuna and three times as large as albacore tuna; dolphinfish also consumed the greatest range of prey sizes. Results quantify dolphinfish trophic interactions in the western Atlantic near the northern extent of their geographical range, and are relevant for ecosystem-based management of the offshore pelagic guild in the context of shifting fish populations and fisheries in response to climate and ecological change.

## Introduction

Dolphinfish (*Coryphaena hippurus*) are an abundant, epipelagic predator found globally in tropical and warm temperate oceans (Gibbs and Collette 1959; Palko et al. 1982; Oxenford 1999). Throughout their Atlantic range, dolphinfish are considered an economically important species, supporting both recreational and commercial fisheries (Oxenford and Hunte 1999; Thompson 1999; Farrell et al. 2014). In the western Atlantic, dolphinfish range from Brazil to Nova Scotia and exhibit strong seasonal pulses in abundance in waters of the Caribbean, the Gulf of Mexico, and the U.S. South Atlantic (Oxenford 1999; Farrell et al. 2014). In recent decades, dolphinfish landings have risen globally (Thompson 1999; Whoriskey et al. 2011), with exponential increases in catches in western Atlantic waters since the 1950s and a concurrent rise in economic importance (NOAA 2010; Whoriskey et al. 2011). Increased landings are likely due to a combination of factors, including changes in targeted populations by fisheries, oceanographic shifts associated with climate change, and release from predation or competition by apex predators such as billfish, as has been demonstrated in the Pacific Ocean (Kitchell et al. 1999, 2002; Polovina et al. 2009; Ward and

---

Communicated by C. Harrod.

---

Reviewed by J. Logan and an undisclosed expert.

---

✉ Amy K. Teffer  
ateffer@uvic.ca

<sup>1</sup> Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003-9285, USA

<sup>2</sup> Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC 28403, USA

<sup>3</sup> Present Address: Department of Biology, University of Victoria, 3800 Finnerty Road, Victoria, BC V8P 5C2, Canada

<sup>4</sup> Present Address: DOI Northeast Climate Science Center, 134 Morrill Science Center, University of Massachusetts, Amherst, MA 01003-9297, USA

Myers 2005; Whoriskey et al. 2011). The Southern New England (SNE) region located off the U.S. Atlantic coast in the western North Atlantic Ocean is an area of seasonally elevated productivity and a feeding ground for a diversity of highly migratory fishes such as dolphinfish and tunas (Chase 2002; Overholtz 2006; ICCAT 2010; Logan et al. 2011). Although dolphinfish can be found as far north as Nova Scotia, Canada, their northern range has been historically limited by the 20 °C isotherm, with occurrences in waters north of Massachusetts described as rare (Gibbs and Collette 1959; Kleisner 2009). However, warming sea surface temperatures reported off the eastern coast of the U.S. during recent years (Levitus et al. 2000; Rayner et al. 2006) favors dolphinfish range expansion and increased residence time at northern latitudes, similar to that observed in the Pacific Ocean (Norton 1999; Farrell et al. 2014).

Compared with other highly migratory species, dolphinfish have relatively short life spans of <4 years (Schwenke and Buckel 2008) and achieve incredibly rapid growth rates in their first year of life (Oxenford 1999). Dolphinfish feed continuously throughout the day and night (Massuti et al. 1998; Oxenford and Hunte 1999; Young et al. 2010; Merten et al. 2014a) and are reported to consume nearly 6 % of their body weight per day as adults, with growth rates estimated as high as 4.71 mm/day (Oxenford and Hunte 1999; Schwenke and Buckel 2008). The energetic demands imposed by this “life in the fast lane” strategy make dolphinfish influential predators capable of impacting prey population dynamics (Oxenford 1999; Oxenford and Hunte 1999; Olson and Galván-Magaña 2002). In addition, their generalist and opportunistic foraging habits may provide dolphinfish with a competitive advantage over other predators that share the same environment. Dolphinfish foraging habits and interactions with co-occurring species such as tunas and wahoo (*Acanthocybium solandri*) have been described in the Pacific (Bertrand et al. 2002; Young et al. 2010; Baque-Menoscal et al. 2012), Caribbean (Oxenford and Hunte 1999), Central Atlantic (Oxenford 1999; Logan and Lutcavage 2013), and southern Atlantic Oceans (Rudershausen et al. 2010); however, little is known about their trophic role near the northern extent of their range along the Atlantic coast in SNE waters.

Several species of tuna are known to school with dolphinfish and follow similar migration pathways along the Atlantic coast, including yellowfin (*Thunnus albacares*) and albacore (*T. alalunga*) tunas (ICCAT 2010). Despite their commercial importance, ecological studies of these tuna species have also been deficient in the western North Atlantic compared to other ocean basins (Bertrand et al. 2002; Consoli et al. 2008; Pusineri et al. 2008; Goñi et al. 2011; Allain et al. 2012). For example, albacore tuna recruitment has shown sharp declines since the

mid-twentieth century in the Atlantic Ocean, but few studies have been conducted to evaluate potential trophic interactions that may be influencing their population dynamics (ICCAT 2010; NOAA 2010). Matthews et al. (1977) provides one of the few dietary examinations of yellowfin and albacore tuna diets in the western Atlantic and notes reliance on *Sargassum*-associated and upper mesopelagic fish species as primary prey, respectively. Considerably, more research has been conducted in the western Atlantic on bluefin tuna and characterizes a very different suite of prey species as seasonally important, including those typically found in continental shelf waters such as Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes* spp.), and Atlantic mackerel (*Scomber scombrus*) (Matthews et al. 1977; Chase 2002; Estrada et al. 2005; Logan et al. 2011, 2015). Collectively, these studies indicate clear differences in prey resource use among *Thunnus* species and show dolphinfish were historically consumed by yellowfin tuna (Matthews et al. 1977).

Quantification of resource use and partitioning among top predators is needed to understand the structure and function of offshore marine communities, to trace trophic pathways of energy and contaminants, and are research priorities for ecosystem-based management (Link 2004; Buckel et al. 1999; Teffer et al. 2014). A paired approach of stomach content and stable isotope analyses has been extensively used to provide comprehensive evaluations of the trophic ecology (Olson et al. 2010; Logan et al. 2011, 2015; Butler et al. 2015) and niche partitioning of marine predators (Pusineri et al. 2008; Staudinger et al. 2014). Stomach content analysis provides direct observations of the suite of prey species and sizes a predator is consuming, while measurements of stable carbon and nitrogen isotopes in fish muscle and other tissues reflect assimilated diet information over relatively longer spatiotemporal scales (MacNeil et al. 2005; Fry 2006; Olson et al. 2010; Madigan et al. 2012). Stable isotope analysis is an especially useful tool to delineate trophic relationships in species such as large pelagic predators where obtaining numerous stomach samples may not be feasible (Olson et al. 2010).

Using this paired approach, the present study aimed to (1) describe the food habits of dolphinfish and co-occurring yellowfin and albacore tunas to identify important and shared prey and quantify predator–prey body size relationships, and (2) evaluate the extent of trophic niche overlap and potential means of segregation in foraging habits among these three predatory species. Knowledge of predator reliance on seasonal and regional prey resources will provide insight into migratory patterns as well as the influence of prey resources on growth, condition, reproductive output, and ultimately recruitment success (Chase 2002; Overholtz 2006; Golet et al. 2007).

## Methods

### Sample collection

Fish were collected at recreational fishing tournaments and from charter fishing boats operating out of Cape Cod and the Islands of Massachusetts between the months of July and October, 2007–2010. Fish were caught by anglers using rod and reel, generally fishing in the New England Canyons located at the shelf–slope break between approximately 0900 and 1500 hours (Eastern Daylight Time). There is no minimum size restriction on recreationally harvested dolphinfish or albacore tuna in SNE. The minimum size restriction for yellowfin tuna landed in Massachusetts is 70 cm FL, and thus conclusions and implications of the results of this study are restricted to yellowfin of equal or greater sizes. Fish were measured as curved fork length (FL  $\pm$  1.0 mm), stomachs were removed dockside, and approximately a 2.5  $\times$  2.5 cm sample of muscle tissue was removed from just posterior to the dorsal fin of each fish. All samples were placed on ice and then frozen until stomach content, and stable isotope analyses were conducted in the laboratory.

### Stomach content analysis and diet metrics

All prey items recovered from predator stomachs were sorted by major taxonomic group (cephalopod, crustacean, fish, and other invertebrates) and further identified to the level of family (and species when possible) using hard parts such as bones, otoliths, and beaks with the aid of published guides (Robins et al. 1986; Clarke 1996; Parisi-Baradad et al. 2010). Stomachs containing only bait were not included in stomach content analysis. Individual prey items were weighed ( $\pm$ 1.0 g) and counted; intact cephalopod, crustacean, and fish prey were then measured ( $\pm$ 1.0 mm) as mantle length (ML), carapace width (CW), or total length (TL). Body sizes of highly digested prey were estimated from hard parts such as fish jaws or cephalopod beaks using morphometric equations (Clarke 1996; Scharf et al. 1998a; Staudinger et al. 2009, 2013a).

Species accumulation curves were used to evaluate whether an adequate sample size had been collected for a comprehensive description of each predator's diets using an approach outlined by Cook and Bundy (2011). Major prey families were classified as present or absent in a predator diet. Using the *vegan* and *sfsmisc* packages in the R software package version 2.10.0 (R Development Core Team Year 2012), the "random" method (subsampling without replacement) was applied to identify the mean curve and standard deviation (Gotelli and Colwell 2001). Following the guidelines of Cook and Bundy (2011), prey richness

is considered unlikely to increase with further sampling if the curve reaches an asymptote at an x-axis value less than or equal to the sample size collected for that predator (i.e., sample size is sufficient to capture dietary niche breadth). Species accumulation curves were considered to reach an asymptote if the minimum derivative (md) of the curve at the collected sample size was less than the predetermined cutoff value (md < 0.050).

The relative contribution of each prey type to each predator's diet was quantified by mean weight (%MW), mean number (%MN), and the frequency of occurrence (%O) at the level of prey type and family (Logan and Lutcavage 2013; Butler et al. 2015). Each metric provides information pertinent to different aspects of feeding ecology. Briefly, composition by mass relates to nutritional prey base, prey number is associated with feeding behavior (schooling vs. solitary prey) and prey occurrence is a reliable indicator of population-level feeding ecology and prey availability (Macdonald and Green 1983; Cortés 1997). Prey richness, defined here as the number of unique prey families within a predator diet, can be used to describe how generalistic a predator is.

An index of relative importance (%IRI) simultaneously accounts for multiple diet metrics, such as weight, number, and frequency of occurrence, and lessens some of the biases of individual dietary components (Cortés 1997). For example, hard structures, such as fish otoliths and cephalopod beaks, can accumulate in stomachs, inflating the importance of those species in numerical and frequency of occurrence estimates (Santos et al. 2001). To facilitate comparisons among predator species IRI was determined following Pinkas et al. (1971):

$$\text{IRI} = (\%MN + \%MW)\%O$$

The IRI value was then transformed into a percent value (%IRI) for direct comparison of results with previous studies (Cortés 1997). %IRI calculations were made by prey type, and prey family; however, prey that could not be identified to the family level (e.g., unidentified fish) were excluded from %IRI calculation at the level of family, but included for %IRI calculation by prey type. Long-term feeding habits were characterized by pooling data across sampling years. Inter-annual variation in prey composition was also assessed using prey weight data and relative importance of major prey types within each sampling year. Prey families that occurred in three out of the four sampling years were deemed important to predator population-wide food habits and used to measure dietary niche width for comparison across predator species using the Shannon–Wiener index ( $H'$ ):

$$H' = \sum p_i \log(p_i)$$

where  $p_i$  is the proportion of the prey (%O) in the diet that belongs to the  $i$ th prey taxon. Compositional diet overlap among predator species was tested using the same set of prey families with a proportional similarity index developed by Schoener (1974):

$$\alpha = 1.0 - 0.5 \sum |p_{ij} - p_{ik}|$$

where  $p_{ij}$  is the %MW of prey family  $i$  in the diet of predator  $j$  and  $p_{ik}$  is the %MW of that same prey family in predator  $k$ . The value  $\alpha$  ranges from 0 to 1 (0 = no overlap, 1 = complete overlap).

### Predator–prey body size relationships

Predator–prey body size distributions and mean prey sizes by type were compared among predators using a Kolmogorov–Smirnov test (KS), and among sampling years using a Mann–Whitney  $U$  test (MWU). Nonparametric methods were necessary due to the non-normality and heteroscedasticity of prey length data. Predator–prey body size data were graphed as scatter plots and evaluated using ordinary least-squares (OLS) and quantile regression techniques. Quantile regression was used in conjunction with OLS to describe changes in the minimum and maximum prey size in addition to changes in the mean size of prey consumed by predators with growth (Scharf et al. 1998b; Ménard et al. 2006). Quantiles were chosen based on sample sizes as recommended in Scharf et al. (1998b) and Rogers (1992); minimum and maximum slopes were compared using a modified ANOVA to identify changes in absolute prey sizes for each prey type with increasing predator size. Ontogenetic patterns in relative prey size were also compared using a modified ANOVA to assess whether the size-based trophic niche breadth of each predator converged, diverged, or was constant with growth by quantifying differences in minimum and maximum slopes (Scharf et al. 2000; Juanes 2003). Relative prey size rather than absolute was used to compare size-based feeding habits across predators using prey–predator size ratios (PPSR = prey length/predator length) and their relationship with predator body size. Due to the relatively low sample size of albacore tuna, there were insufficient data to evaluate quantile body size relationships for this predator. Therefore, only OLS was used to describe albacore tuna predator–prey size relationships. All quantile evaluations were carried out using the *quantreg* library in Program R (Koenker 2012).

### Stable isotope analyses

Muscle tissue samples from a subset of individuals from dolphinfish ( $N = 22$ ), yellowfin tuna ( $N = 21$ ), albacore tuna ( $N = 10$ ), and baseline organisms ( $N = 3$ ) were

thawed, rinsed with DI water, dried in an oven at 65 °C for  $\geq 48$  h, and homogenized using a mortar and pestle. Aliquots of homogenized tissue of approximately 0.50 mg were measured into 4 × 6 mm tin cups and analyzed for  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , %N, and %C. Tissues were flash-combusted (Costech ECS4010 elemental analyzer), and ratios of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) stable isotopes were analyzed on a Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer (CFIRMS) at the Center for Marine Science at the University of North Carolina Wilmington. Raw  $\delta$  values were normalized using depleted and enriched glutamic acid reference materials USGS-40 and USGS-41. Sample precision was within  $<0.2$  ‰ ( $1\sigma$ ) for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ .

Stable isotope abundances are expressed in  $\delta$  notation in per mille units (‰), according to the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding ratio  $^{13}\text{C}:^{12}\text{C}$  or  $^{15}\text{N}:^{14}\text{N}$ . The  $R_{\text{standard}}$  values were based on the Vienna PeeDee Belemnite (VPDB) for  $^{13}\text{C}$  and atmospheric  $\text{N}_2$  for  $^{15}\text{N}$ . Muscle tissue  $\delta^{13}\text{C}$  values were corrected for lipid content a posteriori using (muscle) tissue-specific mathematical corrections based on C–N ratios within each sample (Fry 2006; Logan et al. 2008).

### Trophic position and isotopic niche breadth

Trophic position was estimated for each predator using  $\delta^{15}\text{N}$  values and following the equation:

$$\text{TP} = \lambda + \frac{\delta^{15}\text{N}_{\text{Secondary consumer}} - \delta^{15}\text{N}_{\text{Base}}}{\Delta n}$$

where secondary consumers were dolphinfish and tunas, and euphausiids from regional waters were used as a base(line) reference organism. Euphausiids were assigned a  $\lambda$  (TP) value of 2.55 following Kline (2002).  $\Delta n$  is the diet–tissue discrimination factor for  $\delta^{15}\text{N}$  and was assumed to be 2.1 ‰ based on values estimated for yellowfin tuna muscle tissues (Post 2002; Graham 2008). Euphausiids were chosen for calculations of trophic position because they were found in all three predator diets and have been described as a representative species of pelagic environments (Kline 2002). Comparisons of trophic positions among predators were conducted using a one-way ANOVA. In addition,  $\delta^{15}\text{N}$  values were evaluated as a function of predator FL using linear regression to determine how trophic position changed with growth.

Bayesian ellipses were used to calculate and evaluate differences in isotopic niche widths between dolphinfish and tunas [Stable Isotope Bayesian Ellipses in R (SIBER); Jackson et al. 2011]. Using this approach, isotopic niche width is measured as the standard ellipse areas (SEA) in

**Table 1** Sample sizes, mean  $\pm$  standard error (SE), and range of curved fork length (FL; cm) for each study species

	Sample size					FL (cm)	
	2007	2008	2009	2010	Total	mean ( $\pm$ SE)	Range
Dolphinfish	53	15	25	64	157	72.0 ( $\pm$ 1.1)	33.0–104.0
Yellowfin tuna	34	10	17	72	133	107.0 ( $\pm$ 1.4)	69.2–136.0
Albacore tuna	11	6	5	4	26	98.3 ( $\pm$ 1.3)	83.8–113.0
Totals	98	31	47	140	316	–	–

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  space and is equivalent to standard deviations (SD) in univariate analyses. Standard ellipses were corrected for small sample sizes ( $\text{SEA}_c$ ) to provide a more robust comparison of the degree of isotopic niche overlap among the three predators, where  $\text{SEA}_c$  contains approximately 40 % of the isotopic data and represents the mean core area of each species' isotopic niche (Jackson et al. 2011, 2012). Overall niche diversity was calculated as the total area (TA) of the convex hull, which encompasses all data points for each species (Layman et al. 2007; Jackson et al. 2012). All metrics were calculated using the R statistical package SIAR (Parnell et al. 2010).

## Results

A total of 316 stomachs were collected from dolphinfish ( $N = 157$ ), yellowfin tuna ( $N = 133$ ), and albacore tuna ( $N = 26$ ) (Table 1). Of the three predators, dolphinfish was the smallest in body size on average ( $72.0 \pm 1.1$  cm FL), yellowfin tuna the largest ( $107.0 \pm 1.4$  cm FL), and albacore tuna was intermediate ( $98.3 \pm 1.3$  cm FL). Frequencies of empty stomachs for dolphinfish, yellowfin tuna, and albacore tuna were 8.3, 7.5 and 3.8 %, respectively (Table 2). The species accumulation curve for dolphinfish reached an asymptote for the sample size collected ( $\text{md} = 0.046$ ; Fig. 1) and marginally surpassed the a priori cutoff value of 0.05 for yellowfin tuna ( $\text{md} = 0.055$ ). The species accumulation curve for albacore tuna did not reach an asymptote ( $\text{md} = 0.241$ ). Results suggest adequate sample sizes were obtained for dolphinfish and likely for yellowfin tuna, but additional collections are still needed to fully assess the albacore diet in this region.

## Diet composition

Fish prey constituted almost half of dolphinfish diets by weight (48 %MW) and number (39 %MN) and comprised a wide diversity of teleosts including Carangidae (6 %MW), Monacanthidae (4 %MW), Dactylopteridae (4 %MW), Clupeidae (2 %MW), Scombridae (2 %MW) and Gempylidae (2 %MW) (Table 2). Cephalopods (33 %MW) also contributed substantially to mean prey weight and included the squids Ommastrephidae (22 %MW) and Loliginidae

(5 %MW). Crustaceans were numerically abundant prey in dolphinfish diets (37 %MN) and consisted primarily of post-larval hermit crabs (Paguroidea; 20 %MN), amphipods (5 %MN) and euphausiids (4 %MN). Prey occurrence was relatively consistent across the three major prey types in dolphinfish diets, though fish were the most frequent (74 %O) followed by crustaceans (65 %O) and cephalopods (51 %O). Prey belonging to the families Ommastrephidae (42 %O), Paguroidea (37 %O), and Carangidae (20 %O) were most common overall in dolphinfish diets.

Cephalopods were the most important prey to yellowfin tuna diets by weight (47 %MW) and number (44 %MN), primarily due to contributions by ommastrephid squids (32 %MW; 28 %MN). Fish prey contributed an additional 38 % by weight from such families as Dactylopteridae (5 %MW), Scombridae (3 %MW) and Stromateidae (3 %MW). Fish prey (26 %MN) and small crustaceans (29 %MN), such as euphausiids (8 %MN) and amphipods (8 %MN), contributed almost equally to yellowfin tuna diets numerically. The most frequently occurring prey across yellowfin tuna diets included Ommastrephidae (74 %O), Amphipoda (31 %O), Brachyura (29 %O), and Dactylopteridae (28 %O).

Albacore tuna were similar to yellowfin in their diet composition by prey type and primary consumption of ommastrephid squids (33 %MW; 29 %MN; 68 %O). Paguroidea, Amphipoda, and Euphausiidae were the most important crustaceans in albacore diets by weight (6–12 %MW) and number (8–13 %MN). Cephalopods and fish were the most frequently occurring prey types in albacore diets ( $\geq 80$  %O) and included Ommastrephidae (68 %O), other squids (20 %O), Dactylopteridae (16 %O), and Argonautidae (12 %O).

Ommastrephidae and Paguroidea were identified as primary prey of dolphinfish (44 and 32 %IRI, respectively) and albacore tuna (74 and 9 %IRI, respectively), while Ommastrephidae (70 %IRI), Amphipoda (7 %IRI), Dactylopteridae (5 %IRI), and Euphausiidae (5 %IRI) were most important to the diets of yellowfin tuna. Shortfin squid (*Illex illecebrosus*) was identified as the primary ommastrephid consumed and the single most important prey species overall in dolphinfish and tuna diets.

Dolphinfish, yellowfin tuna, and albacore tuna body size was relatively consistent across sampling

**Table 2** Mean percent by number (%MN) and weight (%MW)  $\pm$  standard deviation (SD), percent occurrence (%O), and relative importance (%IRI) of prey families for each predator species [IRI = (%MN + %MW)  $\times$  %O, shown as relative percent by major prey type and by family]

	Dolphinfish				Yellowfin tuna				Albacore tuna			
	%MW	%MN	%O	%IRI	%MW	%MN	%O	%IRI	%MW	%MN	%O	%IRI
<b>Fish</b>	<b>47.5 <math>\pm</math> 44.0</b>	<b>38.8 <math>\pm</math> 37.0</b>	<b>73.6</b>	<b>23.4</b>	<b>37.7 <math>\pm</math> 39.7</b>	<b>25.8 <math>\pm</math> 28.8</b>	<b>76.4</b>	<b>16.8</b>	<b>31.2 <math>\pm</math> 37.4</b>	<b>25.6 <math>\pm</math> 33.1</b>	<b>80.0</b>	<b>1.0</b>
Ammodytidae					0.1 $\pm$ 0.8	0.4 $\pm$ 2.2	3.3	–				
Belonidae					0.8 $\pm$ 9.1	0.2 $\pm$ 2.5	1.6	–				
Carangidae	6.4 $\pm$ 20.1	4.7 $\pm$ 14.0	20.1	3.2	0.1 $\pm$ 0.9	0.5 $\pm$ 3.8	4.1	–				
Clupeidae	2.1 $\pm$ 12.7	1.6 $\pm$ 10.4	3.5	0.2	1.0 $\pm$ 5.6	2.1 $\pm$ 11.4	4.1	0.3				
Cyprinodontidae					0.8 $\pm$ 9.2	0.8 $\pm$ 9.2	0.8	–				
Dactylopteridae	3.9 $\pm$ 14.9	2.9 $\pm$ 9.8	13.2	0.6	5.4 $\pm$ 15.0	6.0 $\pm$ 15.2	27.6	2.0	1.6 $\pm$ 4.9	1.4 $\pm$ 5.6	16.0	0.5
Exocoetidae					1.4 $\pm$ 11.1	0.3 $\pm$ 2.2	1.6	–				
Fistulariidae	0.8 $\pm$ 6.5	0.6 $\pm$ 4.1	2.8	–	0.4 $\pm$ 3.2	0.3 $\pm$ 1.7	4.1	–				
Gadidae	0.7 $\pm$ 8.4	0.4 $\pm$ 4.2	0.7	–								
Gempylidae	1.6 $\pm$ 10.5	1.0 $\pm$ 8.7	2.8	0.4	0.4 $\pm$ 4.1	–	1.6	–				
Haemulidae									–	0.1 $\pm$ 0.3	4.0	–
Hemiramphidae	1.3 $\pm$ 10.6	0.3 $\pm$ 3.1	1.4	0.1	0.5 $\pm$ 3.7	0.1 $\pm$ 0.8	1.6	–				
Holocentridae	0.5 $\pm$ 2.6	0.5 $\pm$ 2.6	4.9	0.1	1.2 $\pm$ 7.9	0.4 $\pm$ 1.9	5.7	–				
Istiophoridae	0.4 $\pm$ 4.7	0.2 $\pm$ 2.3	0.7	–								
Macrouridae					–	–	0.8	–				
Merlucciidae	1.0 $\pm$ 8.9	0.9 $\pm$ 6.5	2.1	0.2	0.2 $\pm$ 1.9	0.1 $\pm$ 0.8	4.1	–				
Monacanthidae	4.2 $\pm$ 17.7	2.9 $\pm$ 13	8.3	0.4	1.1 $\pm$ 6.8	0.6 $\pm$ 2.7	12.2	0.1	–	–	4.0	–
Mugilidae	0.7 $\pm$ 8.5	0.9 $\pm$ 8.6	1.4	–								
Myctophidae					0.8 $\pm$ 7.1	0.4 $\pm$ 3.7	3.3	–				
Nomeidae	0.7 $\pm$ 6.2	1.3 $\pm$ 6.5	5.6	0.1	0.5 $\pm$ 2.8	0.4 $\pm$ 2.0	8.1	–	0.2 $\pm$ 0.8	0.3 $\pm$ 1.1	8.0	–
Ogcocephalidae					–	–	0.8	–				
Percichthyidae	–	0.1 $\pm$ 1.2	0.7	–								
Phycidae					0.4 $\pm$ 4.8	0.2 $\pm$ 2.0	2.4	–				
Pleuronectidae					–	–	0.8	–				
Polymixidae	0.6 $\pm$ 7.2	0.4 $\pm$ 4.2	0.7	–								
Pomatomidae	1.0 $\pm$ 9.0	0.4 $\pm$ 2.9	2.1	0.1	0.8 $\pm$ 8.7	0.1 $\pm$ 1.2	0.8	–				
Scomberesocidae					1.2 $\pm$ 9.2	0.3 $\pm$ 2.3	2.4	0.1				
Scombroidae	1.9 $\pm$ 12	0.6 $\pm$ 3.2	4.9	0.3	2.9 $\pm$ 14.6	0.9 $\pm$ 5.0	5.7	0.5				
Serranidae	0.2 $\pm$ 1.7	0.1 $\pm$ 1.6	2.1	–	–	0.3 $\pm$ 3.7	0.8	–				
Sphyraenidae					0.1 $\pm$ 1.3	0.1 $\pm$ 1.0	0.8	–				
Stromateidae	0.1 $\pm$ 0.9	0.5 $\pm$ 3.2	3.5	–	2.6 $\pm$ 11.3	1.1 $\pm$ 5.9	8.1	0.3				
Syngnathidae	0.3 $\pm$ 2.7	0.6 $\pm$ 4.5	4.2	–	0.8 $\pm$ 4.9	0.3 $\pm$ 1.4	4.9	–				
Tetraodontidae	1.1 $\pm$ 7.2	1.9 $\pm$ 9.3	9.0	0.4	1.1 $\pm$ 5.7	1.5 $\pm$ 7.7	9.8	0.2				
Triglidae					–	0.1 $\pm$ 0.6	1.6	–				
Zeidae	0.1 $\pm$ 1.3	0.1 $\pm$ 1.1	0.7									
Unclassified	17.4 $\pm$ 32.1	15.8 $\pm$ 25.2	62.5		12.9 $\pm$ 24.7	8.2 $\pm$ 13.5	65.9		29.3 $\pm$ 37.8	23.8 $\pm$ 33.5	84.0	
<b>Cephalopod</b>	<b>32.9 <math>\pm</math> 41.8</b>	<b>23.6 <math>\pm</math> 34.3</b>	<b>51.4</b>	<b>28.3</b>	<b>46.7 <math>\pm</math> 42.3</b>	<b>44.3 <math>\pm</math> 37.3</b>	<b>85.4</b>	<b>56.6</b>	<b>42.2 <math>\pm</math> 40.6</b>	<b>39.7 <math>\pm</math> 35.1</b>	<b>84.0</b>	<b>56.6</b>
Argonautidae	1.5 $\pm$ 10.3	1.3 $\pm$ 8.8	6.3	0.1	1.4 $\pm$ 9.6	2.7 $\pm$ 10.5	20.3	0.4	0.3 $\pm$ 1.5	0.8 $\pm$ 2.5	12.0	0.1
Chiroteuthidae	–	0.1 $\pm$ 1.2	0.7	–								
Enoploteuthidae					0.6 $\pm$ 6.7	0.5 $\pm$ 5.0	0.8	–				
Histioteuthidae					–	0.1 $\pm$ 0.8	0.8	–				
Loliginidae	4.5 $\pm$ 19.2	2.6 $\pm$ 13.2	6.9	1.4	4.4 $\pm$ 16.8	3.8 $\pm$ 13.4	12.2	1.2				
Mastigoteuthidae					–	–	1.6	–				
Octopodidae					–	0.4 $\pm$ 2.2	4.9	–	0.1 $\pm$ 0.3	0.5 $\pm$ 2.3	8.0	–
Ommastrephidae	21.7 $\pm$ 36.6	15.6 $\pm$ 28.6	41.7	41.6	31.6 $\pm$ 39.3	28.2 $\pm$ 32.7	74	70.9	32.8 $\pm$ 43.8	29.1 $\pm$ 36.3	68.0	69.2

**Table 2** continued

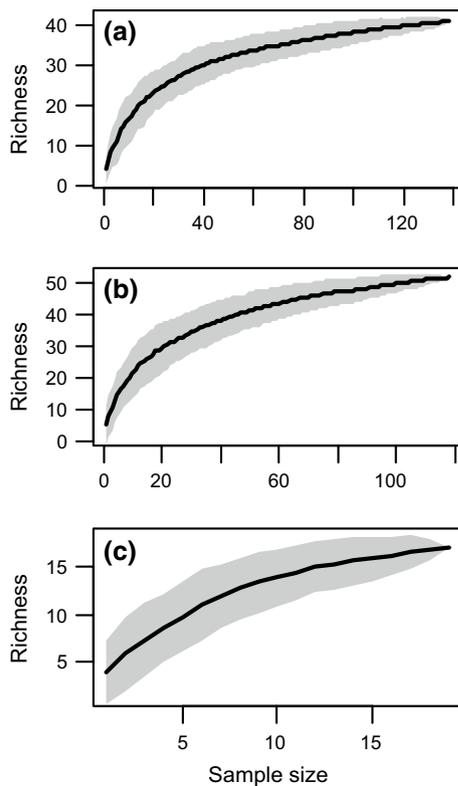
	Dolphinfish				Yellowfin tuna				Albacore tuna			
	%MW	%MN	%O	%IRI	%MW	%MN	%O	%IRI	%MW	%MN	%O	%IRI
Onychoteuthidae					–	0.1 ± 0.7	0.8	–				
Pholidoteuthidae					–	–	0.8	–				
Sepioloidea					–	–	1.6	–				
Teuthoidea	2.9 ± 12.3	2.0 ± 7.3	14.6	1.1	6.5 ± 20.5	5.4 ± 16.9	21.1	2	2.3 ± 5.9	3.4 ± 13.7	20.0	0.8
Unclassified	2.5 ± 13.7	2.2 ± 10.6	9.0		2.2 ± 9.3	3.2 ± 10.7	17.9		6.8 ± 15.2	6.0 ± 13.0	36.0	
<b>Crustacean</b>	<b>19.0 ± 31.3</b>	<b>36.6 ± 36.5</b>	<b>64.6</b>	<b>48.2</b>	<b>14.1 ± 28.3</b>	<b>28.6 ± 34.1</b>	<b>56.9</b>	<b>26.6</b>	<b>26.5 ± 39.2</b>	<b>33.9 ± 42.6</b>	<b>44.0</b>	<b>42.3</b>
Amphipoda	3.0 ± 15.5	5.0 ± 19.2	12.5	3.2	4.8 ± 17	8.4 ± 20.7	30.9	9.2	6.4 ± 19.9	9.5 ± 23.4	28.0	10.5
Brachyura	0.4 ± 3.4	1.3 ± 7.1	5.6	0.2	1.4 ± 8.9	6.2 ± 16.3	28.5	3.8	0.3 ± 1.5	2.8 ± 12.6	8.0	0.5
Decapoda	–	0.1 ± 1.1	0.7	–	0.1 ± 0.8	0.4 ± 2.4	6.5	–	0.1 ± 0.5	0.3 ± 0.8	12.0	0.1
Euphausiidae	0.8 ± 3.4	3.9 ± 12.7	13.9	1.0	5.1 ± 17.5	7.9 ± 20.3	22.0	7.9	7.6 ± 22.2	7.5 ± 22.0	20.0	8.0
Idotea	0.6 ± 3.6	2.3 ± 11.2	5.6	0.2	–	0.2 ± 2.1	2.4	–				
Majoidea	0.6 ± 3.8	1.9 ± 7.5	11.1	0.3	0.4 ± 4.1	0.9 ± 6.9	7.3	0.1	0.1 ± 0.4	0.1 ± 0.3	4.0	–
Paguroidea	11.8 ± 26.2	19.7 ± 33.2	36.8	44.3	0.5 ± 2.8	2.2 ± 7.4	21.1	0.5	11.9 ± 27	13.0 ± 29.0	20.0	10.1
Penaeidae	–	0.1 ± 0.6	0.7	–								
Portunidae	1.8 ± 11.1	1.9 ± 8.1	8.3	0.2	0.4 ± 2.6	0.3 ± 2.2	5.7	–	–	0.3 ± 1.6	4.0	–
Unclassified	0.1 ± 1.0	0.7 ± 7.5	2.1		1.3 ± 8.3	2.0 ± 10.1	13.0		–	0.5 ± 2.3	4.0	–
<b>Other invertebrates</b>	<b>0.6 ± 7.1</b>	<b>1.0 ± 6.5</b>	<b>2.8</b>	<b>–</b>	<b>1.5 ± 5.7</b>	<b>1.4 ± 4.7</b>	<b>17.1</b>	<b>–</b>	<b>–</b>	<b>0.7 ± 3.4</b>	<b>4.0</b>	<b>–</b>
Cavoliniidae					0.1 ± 0.7	0.2 ± 0.9	6.5	–				
Cnidaria	–	0.4 ± 4.2	0.7	–	0.3 ± 2.1	0.3 ± 2.6	3.3	–				
Littorinidae	–	–	0.7	–	0.2 ± 2.0	0.1 ± 0.9	2.4	–				
Unclassified	0.6 ± 7.1	0.6 ± 5.1	1.4		0.9 ± 4.4	0.7 ± 3.4	8.1		–	0.7 ± 3.4	4.0	
<b>Non-prey</b>												
Bait			19.1				18.0					
Parasite			5.6				9.8				44.0	
Seaweed			23.6				21.1				4.0	
Trash/incidental			8.3				12.2				0.8	
<b>Empty</b>			<b>8.3</b>				<b>7.5</b>				<b>3.8</b>	

Bold values are subtotals of prey types. Values <0.1 are represented by (–), and zero values are left blank. Unclassified prey was included in the %IRI analysis by prey type (bold) but excluded from %IRI calculation by prey family

years (ANOVA: all  $P > 0.18$ ). Overall prey composition (by %MW and %IRI) was found to vary significantly among sampling years and predators (Fig. 2). For all predators, inter-annual consumption of crustacean prey varied significantly (ANOVA: all  $P < 0.03$ ). In dolphinfish, consumption of fish prey varied significantly among years ( $P = 0.003$ ), but not consumption of cephalopods ( $P = 0.529$ ). Conversely, tunas showed inter-annual variation in the amount of cephalopods consumed ( $P < 0.004$ ), but consumption of fish prey was consistent ( $P > 0.355$ ). Dolphinfish relied heavily on cephalopods and crustaceans during 2007–2008, but their diets shifted to predominantly fish prey, typically associated with *Sargassum* communities, in 2009–2010. Overall dolphinfish dependence on ommastrephid squids showed a marginal but noteworthy decrease from approximately 40 %IRI in 2007, to 35 %IRI in 2008, to 2–20 %IRI during 2009–2010, opposite to the

significant temporal changes in fish prey in their diets. Predation by both tunas on small pelagic crustaceans (e.g., Amphipoda, Euphausiidae) was greatest in 2007 and also in 2008 for albacore. Yellowfin tuna showed a pronounced shift to teuthivory during the 2008 and 2010 sampling years, while albacore diets reflected a similar trend in 2009–2010. Although ommastrephids were the dominant prey in tuna diets during most sampling years, strong dependence on crustacean prey was evident during 2007.

Yellowfin tuna diets showed the highest prey richness of all three predators (Richness = 50;  $H' = 88$  %O). Albacore tuna consumed the fewest prey species overall (Richness = 15;  $H' = 80$  %O), and dolphinfish were intermediate (Richness = 38;  $H' = 85$  %O). Schoener's index of proportional similarity using prey %MW data showed that all predators had high and biologically significant dietary overlap ( $\alpha = 0.82$ – $0.86$ ). Albacore and yellowfin tuna



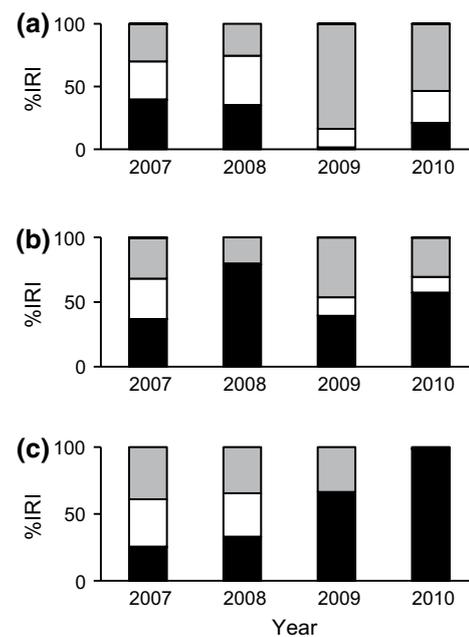
**Fig. 1** Species accumulation curves and confidence intervals for **a** dolphinfish, **b** yellowfin tuna, and **c** albacore tuna. Richness pertains to the number of unique prey items (family)

diets had the greatest overlap ( $\alpha = 0.86$ ), though overlap between dolphinfish and albacore ( $\alpha = 0.84$ ) and yellowfin ( $\alpha = 0.82$ ) tunas was also remarkably high.

### Predator–prey body size relationships

Mean prey size was similar between dolphinfish and yellowfin tuna (6.0 and 6.1 cm, respectively; Table 3) and greater than that of albacore tuna (4.2 cm). The range of prey sizes consumed by dolphinfish (0.2–43.0 cm) was wider than that of yellowfin tuna (0.1–33.0 cm) and albacore tuna (0.3–13.2 cm). Cephalopod prey had the greatest mean length of any prey type and was significantly larger in dolphinfish diets (mean size = 12.7 cm) than in tuna diets (MWU:  $P < 0.01$ ). Crustacean and fish prey length frequency distributions for dolphinfish and tunas were positively skewed, demonstrating consumption of numerous small prey. Crustaceans were the smallest prey overall (mean size = 1.0 cm); however, fish prey length varied greatly among predator species and within predator diets.

Predator–prey size relationships (OLS absolute prey size data) of all prey types combined showed no change in prey size with ontogeny for dolphinfish but a slight increase for yellowfin tuna (Table 4). Differences between the slopes



**Fig. 2** Relative importance (%IRI) of major prey types within each sampling year for **a** dolphinfish, **b** yellowfin tuna, and **c** albacore tuna [ $\text{IRI} = (\%MN + \%MW) \times \%O$ , shown as relative percent]. Bar shading represents the %IRI of cephalopod (black), crustacean (white), and fish (gray) prey in the diets of dolphinfish, yellowfin tuna and albacore tuna collected each year

**Table 3** Mean length  $\pm$  standard deviation (SD) and length range (cm) of prey by major type and predator species

	Dolphinfish	Yellowfin tuna	Albacore tuna
Cephalopod			
Mean $\pm$ SD	12.7 $\pm$ 4.9	8.5 $\pm$ 3.6	5.9 $\pm$ 2.1
Range	(4.4–23.6)	(0.8–26.6)	(0.5–13.2)
Crustacean			
Mean $\pm$ SD	1.0 $\pm$ 0.7	1.0 $\pm$ 0.8	1.0 $\pm$ 0.6
Range	(0.2–43.0)	(0.1–4.6)	(0.3–2.5)
Fish			
Mean $\pm$ SD	5.9 $\pm$ 6.4	5.1 $\pm$ 4.9	1.4 $\pm$ 0.5
Range	(0.8–43.0)	(0.8–33.0)	(1.5–5.1)
All prey combined			
Mean $\pm$ SD	6.0 $\pm$ 6.5	6.1 $\pm$ 4.6	4.2 $\pm$ 2.8

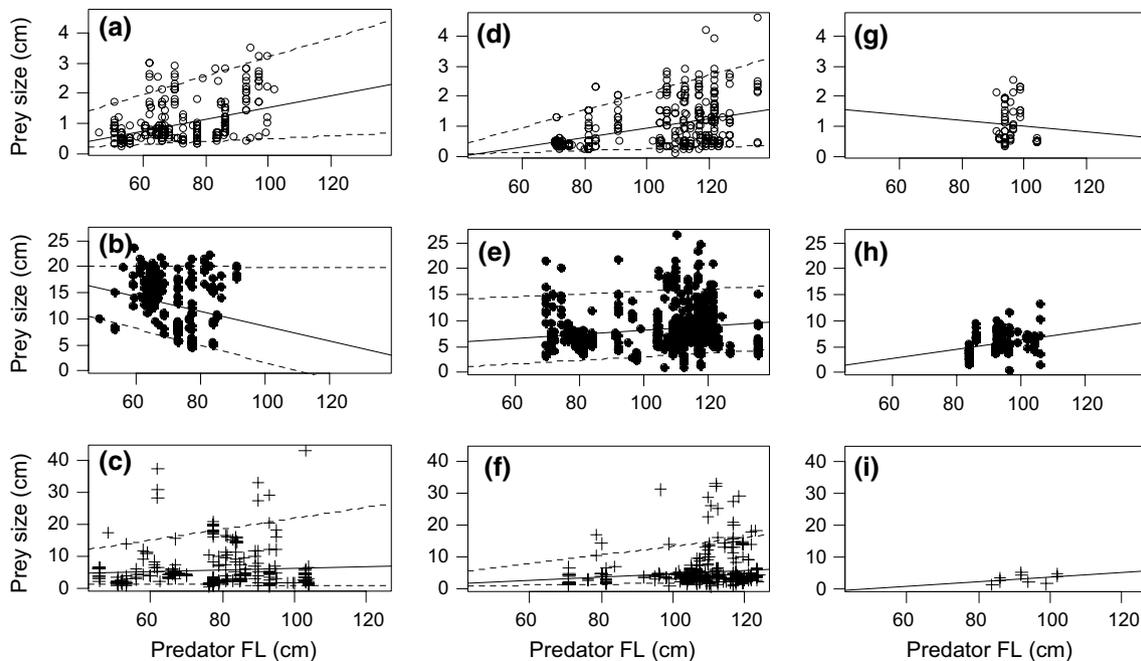
Squid prey were measured as mantle length, decapod prey as carapace width and all other prey as total length

of maximum and minimum quantile of absolute prey size data were not significant for dolphinfish or yellowfin tuna (ANOVA:  $P \geq 0.563$ ). Although coefficients of determination were low, an overall decrease in cephalopod mean prey size with predator growth (OLS) was apparent in dolphinfish diets ( $R^2 = 0.048$ ,  $P < 0.001$ ), while cephalopod prey size increased slightly with yellowfin tuna growth ( $R^2 = 0.027$ ,  $P < 0.001$ )

**Table 4** Quantile (5th and 95th) and ordinary least-squares (OLS) regression equations for all prey combined and by major type in the diets of dolphinfish and yellowfin tuna. Other invertebrates were included in regression equations for all prey types combined, but not by prey type due to low sample sizes

	N	Minimum (5th)	OLS	Maximum (95th)	ANOVA
<b>Dolphinfish</b>					
All prey types	814	$PY = -0.081 + 0.008PD$ $P < 0.001$	$PY = 6.545 - 0.007PD$ $P = 0.675, R^2 < 0.001$	$PY = 17.136 + 0.023PD$ $P = 0.387$	$P = 0.563$
Cephalopod	230	$PY = 17.553 - 0.159PD$ $P = 0.058$	$PY = 22.764 - 0.141PD$ $P < 0.001, R^2 = 0.048$	$PY = 20.320 - 0.003PD$ $P = 0.954$	$P = 0.102$
Crustacean	296	$PY = 0.041 + 0.005PD$ $P < 0.001$	$PY = -0.388 + 0.019PD$ $P < 0.001, R^2 = 0.148$	$PY = 0.151 + 0.031PD$ $P < 0.001$	$P = 0.004$
Fish	287	$PY = 1.303 - 0.001PD$ $P = 0.862$	$PY = 3.955 + 0.025PD$ $P = 0.263, R^2 = 0.004$	$PY = 4.837 + 0.170PD$ $P = 0.261$	$P = 0.257$
<b>Yellowfin tuna</b>					
All prey types	1619	$PY = -0.088 + 0.005PD$ $P < 0.001$	$PY = 0.730 + 0.051PD$ $P < 0.001, R^2 = 0.030$	$PY = 2.683 + 0.016PD$ $P = 0.574$	$P = 0.694$
Cephalopod	905	$PY = -0.411 + 0.035PD$ $P = 0.002$	$PY = 4.336 + 0.039PD$ $P < 0.001, R^2 = 0.027$	$PY = 13.149 + 0.026PD$ $P = 0.498$	$P = 0.820$
Crustacean	322	$PY = -0.021 + 0.003PD$ $P = 0.002$	$PY = -0.593 + 0.015PD$ $P < 0.001, R^2 = 0.147$	$PY = -0.730 + 0.029PD$ $P < 0.001$	$P < 0.001$
Fish	381	$PY = 0.167 + 0.017PD$ $P = 0.016$	$PY = -0.185 + 0.049PD$ $P = 0.012, R^2 = 0.017$	$PY = 0.167 + 0.131PD$ $P = 0.433$	$P = 0.493$

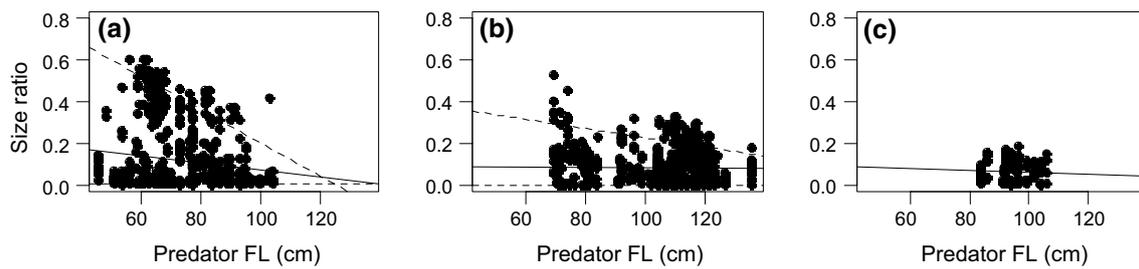
Equations describe the relationship of predator length (PD) to absolute prey length (PY) in centimeters. Significant differences between minimum and maximum quantile slopes are shown in the ANOVA column



**Fig. 3** Predator–prey body size relationships of dolphinfish (a–c), yellowfin tuna (d–f), and albacore tuna (g–i) with crustacean (open circle upper panels), cephalopod (filled circle middle panels), and fish prey (plus symbol lower panels), respectively. Quantile (dashed) and OLS (solid) slopes are included. Note y-axes differ among plots. Slope equations,  $R^2$  and  $P$  values can be found in Table 4

(Fig. 3). Quantile slopes (minimum and maximum) of dolphinfish cephalopod prey sizes were not significantly different from zero. Yellowfin tuna data showed an increase in the

minimum cephalopod prey length with ontogeny, while maximum prey length remained relatively constant. Mean crustacean prey size increased in both dolphinfish and yellowfin



**Fig. 4** Prey–predator body size ratio relationships (all prey types combined) with predator fork length (FL) of **a** dolphinfish, **b** yellowfin tuna, and **c** albacore tuna showing OLS regression (*solid*) lines.

Dolphinfish and yellowfin tuna plots also show minimum (5th) and maximum (95th) quantiles (*dashed*). Slope equations and  $R^2$  and  $P$  values for dolphinfish and yellowfin tuna are shown in Table 5

**Table 5** Sample sizes and equations of OLS and quantile regression (5th and 95th) analyses describing the relationship between relative prey size (PPSR = prey length/predator length) and predator length (PD) for all prey types by predator species

Species	$N$	Minimum	OLS	Maximum	ANOVA
Dolphinfish	814	PPSR = 0.010 + 0.000PD $P = 0.902$	PPSR = 0.238–0.002PD $P < 0.001$ , $R^2 = 0.024$	PPSR = 0.990–0.008PD $P < 0.001$	$P < 0.001$
Yellowfin tuna	1619	PPSR = 0.003 + 0.000PD $P = 0.770$	PPSR = 0.091–0.000PD $P = 0.596$ , $R^2 < 0.001$	PPSR = 0.446–0.002PD $P = 0.002$	$P = 0.001$

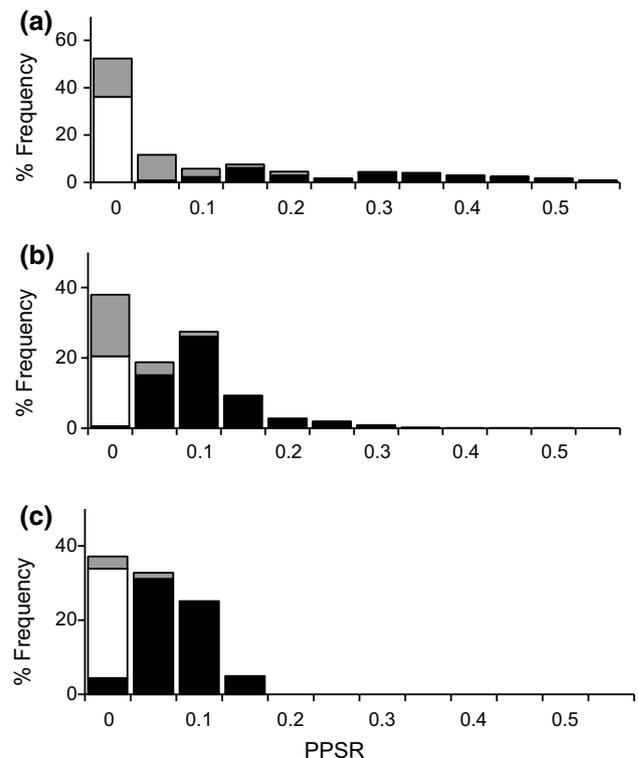
ANOVA significance values refer to the comparison between minimum and maximum quantile slopes of relative prey size relationships

tuna diets with predator growth, though coefficients of determination were low for all OLS relationships (all  $R^2 < 0.15$ ), and a classic “wedge” shape emerged as the maximum crustacean prey size increased with predator size, while minimum prey sizes remained constant (ANOVA:  $P < 0.004$ ). There was a significant increase in minimum fish prey size relative to yellowfin tuna size, but not for maximum prey sizes.

Relative prey–predator body size (PPSR) scatter plots for both dolphinfish and yellowfin tuna showed significant differences between minimum and maximum quantiles (ANOVA:  $P \leq 0.001$ ), suggesting that size-based trophic niche breadths of dolphinfish and yellowfin tuna were converging with predator ontogeny (Fig. 4; Table 5). Although the diets of both tunas and dolphinfish were dominated by relatively small prey, dolphinfish consumed a wider breadth of prey sizes than tunas, especially with respect to cephalopod prey (Fig. 5). The mean ratio of prey body size to predator body size was greatest in dolphinfish diets (11.7 %) followed by yellowfin and albacore tuna diets (8.5 and 6.7 %, respectively).

### Stable isotope analyses

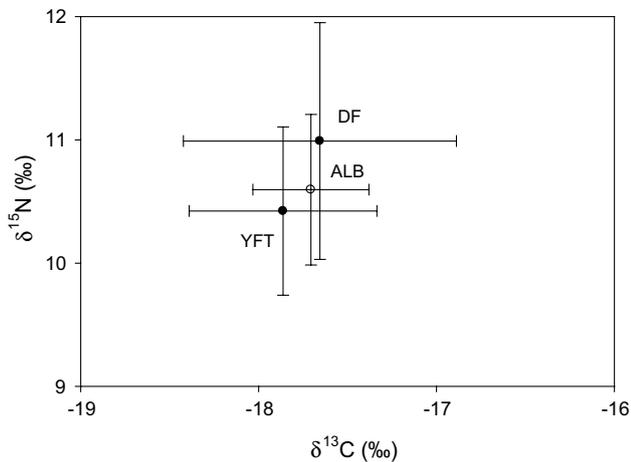
Muscle tissues of all three predators were found to have similar mean  $\delta^{15}\text{N}$  (dolphinfish:  $10.99 \pm 0.96$  ‰; yellowfin:  $10.42 \pm 0.68$  ‰; albacore:  $10.60 \pm 0.61$  ‰),  $\delta^{13}\text{C}$  values (dolphinfish:  $-17.66 \pm 0.77$  ‰; yellowfin:  $-17.86 \pm 0.53$  ‰; albacore:  $-17.71 \pm 0.33$  ‰) ( $P$  values  $> 0.07$ ), and occupy



**Fig. 5** Histograms depicting the percent frequency of relative prey body sizes (PPSR = prey length/predator length) in the diets of **a** dolphinfish, **b** yellowfin tuna, and **c** albacore tuna. Prey type is delineated by shading for fish (*gray*), crustaceans (*white*), and cephalopods (*black*)

**Table 6** Mean  $\pm$  SD  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, C:N ratios, trophic position (TP), core isotopic trophic niche width corrected for small sample sizes ( $\text{SEA}_c$ ), and overall niche diversity (TA) measured in muscle tissues of dolphinfish, yellowfin and albacore tuna

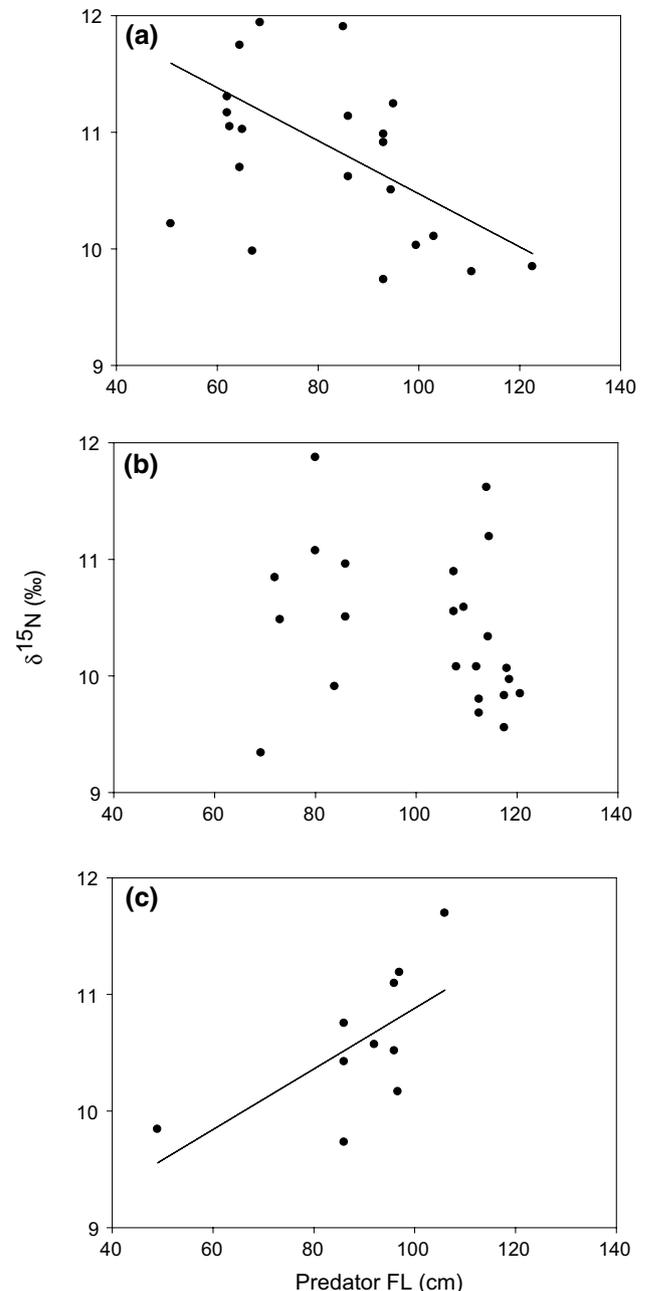
Species	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N	TP	$\text{SEA}_c$	TA
Dolphinfish	22	17.66 $\pm$ 0.77	10.99 $\pm$ 0.96	3.15 $\pm$ 0.12	3.6	2.21	7.48
Yellowfin tuna	21	17.86 $\pm$ 0.53	10.42 $\pm$ 0.68	3.25 $\pm$ 0.20	3.4	1.08	3.12
Albacore tuna	10	17.71 $\pm$ 0.33	10.60 $\pm$ 0.61	3.09 $\pm$ 0.26	3.5	0.69	1.01

**Fig. 6** Stable isotope bi-plot of carbon  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  nitrogen values (mean  $\pm$  SD) of dolphinfish (DF), yellowfin (YFT), and albacore tunas (ALB)

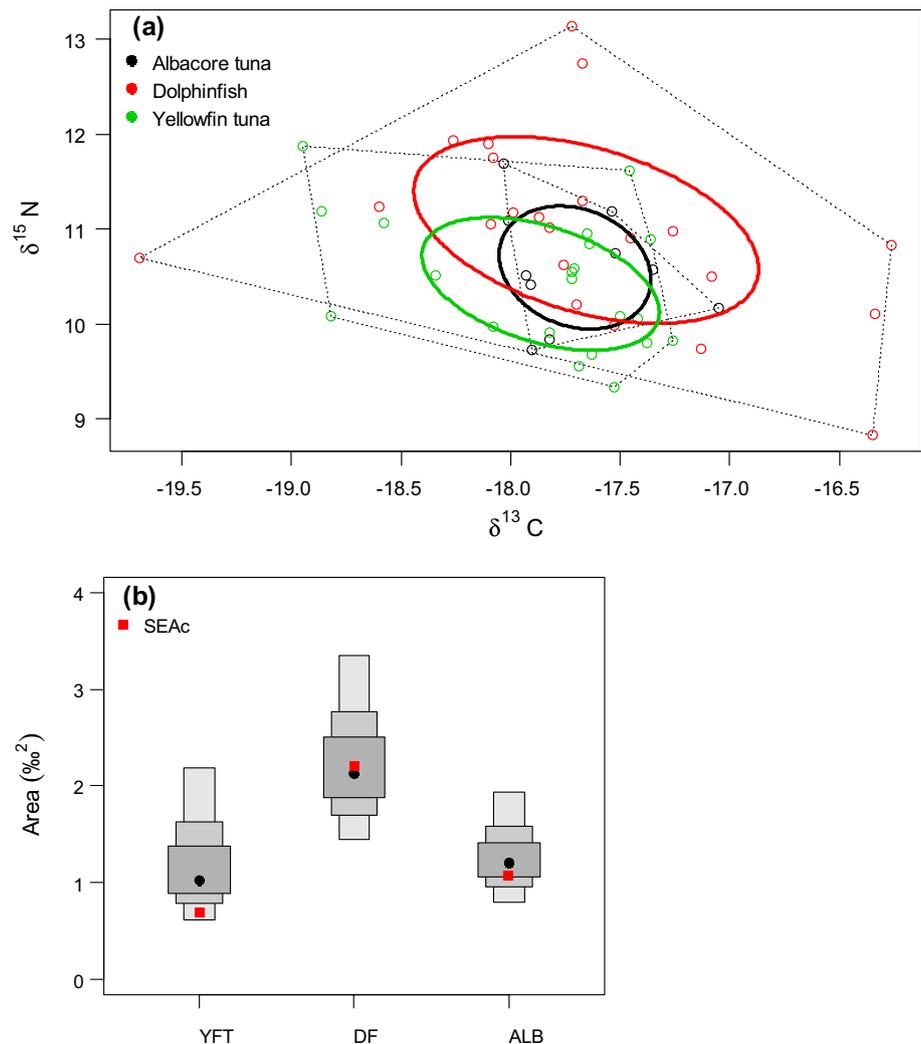
similar trophic positions (3.4–3.6) (Table 6; Fig. 6). Dolphinfish  $\delta^{15}\text{N}$  values exhibited a moderate but significantly decreasing trend with increasing body size ( $R^2 = 0.18$ , slope =  $-0.023$ ,  $P = 0.04$ ); albacore  $\delta^{15}\text{N}$  values increased significantly with growth ( $R^2 = 0.43$ , slope =  $0.026$ ,  $P = 0.04$ ), while yellowfin showed no discernable trend ( $R^2 = 0.06$ , slope =  $-0.009$ ,  $P = 0.25$ ) (Fig. 7). Community metrics revealed the isotopic niche width and overall niche diversity of dolphinfish ( $\text{SEA}_c = 2.21$ ; TA = 7.48) was twice as large as yellowfin tuna ( $\text{SEA}_c = 1.08$ ; TA = 3.12) and substantially larger than albacore tuna ( $\text{SEA}_c = 0.69$ ; TA = 1.01) (Fig. 8; Table 6). Dolphinfish was also found to have higher niche overlap with yellowfin (64.7 %) and albacore tunas (62.9 %) than the two tunas had with each other (53.6 %) (Fig. 8).

## Discussion

This study is the first to quantify the food habits of dolphinfish near the northern extent of their range in the SNE region of the western Atlantic Ocean, and evaluate trophic linkages with co-occurring tunas. Recent evidence suggests that dolphinfish populations may be

**Fig. 7** Muscle stable nitrogen ( $\delta^{15}\text{N}$ ) values in **a** dolphinfish, **b** yellowfin and **c** albacore tuna as a function of predator fork length (FL; cm). Ordinary least squares (OLS) regression lines are shown for significant relationships; slope,  $R^2$  and  $P$  values can be found within the text

**Fig. 8** **a**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bi-plot for albacore tuna (ALB), dolphinfish (DF), and yellowfin tuna (YFT). Standard ellipses corrected for small sample sizes ( $\text{SEAc}$ ) (solid lines) represent the core niche area of each species, and convex hulls of overall niche diversity (dotted lines) encompass all data points. **b** Density plot showing the confidence intervals of the standard ellipse areas. Round points correspond to the mean standard ellipse area, square points to the  $\text{SEAc}$ , and gray shaded boxed areas reflect the 95, 75, and 50 % confidence intervals from lightest to darkest, respectively, for dolphinfish, yellowfin, and albacore tunas



benefiting from a combination of ecological and environmental changes in the SNE region and globally (Kitchell et al. 1999, 2002; NOAA 2010; Whoriskey et al. 2011). As dolphinfish population abundance fluctuates along the US Atlantic coast, there may be important consequences for the species they rely on as primary prey as well as sympatric tunas that occupy similar trophic levels and compete with them for resources. Dolphinfish, yellowfin and albacore tunas consumed many of the same prey species, in particular shortfin squid, small pelagic crustaceans such as amphipods and euphausiids, and juvenile fishes such as flying gurnards often associated with *Sargassum* communities. There was high overlap in dietary and isotopic community metrics, indicating the three predators utilize comparable foraging resources and have similar niches in the SNE region. Overall niche width and diversity of dolphinfish were substantially greater than that of tunas, indicating dolphinfish can exploit a greater range of habitats and forage resources than yellowfin and albacore tunas.

Although there was high isotopic and dietary overlap among dolphinfish and tunas, the combined approach of stomach content and stable isotope analyses revealed that niche partitioning could be occurring through several ecological, biological, and behavioral processes. Slight differences in the species and sizes of prey consumed by each predator were likely influenced by predator-specific morphological and physiological characteristics such as differences in the number and structure of gill rakers (Magnuson and Heitz 1971). The three predators may also segregate their ecological niches by using different spatial and temporal habitats. For example, albacore tuna have been found to dive and feed at greater depths than the more surface-associated dolphinfish and yellowfin tuna (Matthews et al. 1977; Young et al. 2010). Furthermore, recent studies have demonstrated species-specific associations with particular oceanographic features (Kleisner 2009; Kleisner et al. 2010; Goñi et al. 2011). Physiological adaptations and energy conservation strategies play a role in habitat delineation and are important not only for interactions among dolphinfish, yellowfin and albacore

tunas, but also with larger tunas [e.g., bluefin and bigeye (*T. obesus*)], and some billfish that have specializations allowing them to dive and forage at deeper depths for longer time periods (Galli et al. 2009; Merten et al. 2014a). It is important to note that due to the highly migratory nature of dolphinfish and tunas,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, as well as estimates of trophic position may have been influenced by multiple isotopic baselines (Chouvelon et al. 2012). Future studies would benefit from the employment of compound-specific isotopes and analysis of multiple tissue types (e.g., muscle, liver, blood) with different turnover rates to clarify potential inter-specific and spatiotemporal patterns and biases (MacNeil et al. 2005; Popp et al. 2007).

### Foraging habits of dolphinfish and tunas in SNE

Large floating seaweed mats of the genus *Sargassum* serve as habitat for a diverse community and nursery ground for fish and invertebrates and have been shown to be used as a consistent food source for migrating yellowfin tuna and dolphinfish (Rose and Hassler 1974; Rountree 1990; Castro et al. 1999; Dagorn et al. 2006; Casazza and Ross 2008). Surface- and *Sargassum*-associated feeding in yellowfin tuna and dolphinfish was evident from the presence of juvenile prey, especially fishes, from families such as Carangidae, Monacanthidae, Nomeidae, Scombridae, and Tetraodontidae (Casazza and Ross 2008). Analogous prey species have also been documented in dolphinfish and yellowfin tuna diets from southern regions (Rose and Hassler 1974; Oxenford and Hunte 1999; Bertrand et al. 2002; Olson and Galván-Magaña 2002; Rudershausen et al. 2010). Clockwise vortices that form on the north side of the meandering Gulf Stream current can travel north toward the SNE region carrying warm water as well as *Sargassum* mats and associated Gulf Stream fauna within their rotation (Casazza and Ross 2008; Chaudhuri et al. 2009; Naval Research Laboratory 2011). Dolphinfish and yellowfin tuna can remain associated with *Sargassum* mats for weeks at a time (Dagorn et al. 2006; Castro et al. 1999; Farrell et al. 2014). The presence of subtropical and tropical fishes of *Sargassum* communities in SNE predator diets is consistent with historical information available from Matthews et al. (1977) and emphasizes the importance of the Gulf Stream and its potential to support dolphinfish and tunas on a tropical food base even at temperate latitudes.

Albacore tuna have been well studied in the Mediterranean Sea, Northeast Atlantic and Pacific Oceans (Bertrand et al. 2002; Consoli et al. 2008; Pusineri et al. 2008; Goñi et al. 2011; Allain et al. 2012; Cosgrove et al. 2014). However, to the best of our knowledge, this study represents the majority of data describing albacore tuna trophic ecology in the SNE region since Matthews et al. (1977). Additional studies of albacore tuna in the western North Atlantic

are required as stocks and recruitment have shown sharp declines since the mid-20th century (ICCAT 2010; NOAA 2010). Although a limited number of albacore tuna were sampled in the present study, the combination of diet and stable isotope data do allow for some insight into albacore tuna foraging habits and trophic niche overlap with dolphinfish and yellowfin tunas. The strong dependence of albacore tuna on crustacean and cephalopod prey in the SNE region is consistent with diet descriptions conducted in the eastern Atlantic (Pusineri et al. 2008) and Pacific Oceans (Bertrand et al. 2002; Young et al. 2010). Teleosts were less important to albacore tuna in SNE relative to other regions such as the Mediterranean Sea (Consoli et al. 2008), though teleosts may have been underrepresented due to the advanced digestive state of fish prey in many of the stomachs examined. Recent studies in nearby waters of the Central Atlantic reported that albacore tuna consumed equal amounts of cephalopod and piscine prey, and considerably lower amounts of crustaceans than was found in the present study and eastern Atlantic region (Logan and Lutcavage 2013). Albacore tuna have been found to occupy a similar trophic position as yellowfin and juvenile bluefin tunas in the region (Estrada et al. 2005), but a slightly higher trophic position compared to dolphinfish and yellowfin tuna in the Central Atlantic (Logan and Lutcavage 2013).

The majority of prey found in albacore tuna stomachs was in a more degraded condition than that of yellowfin tuna and dolphinfish. Considering the digestion state and the fact that fish were primarily landed by anglers during the daytime is consistent with the findings of Pusineri et al. (2008), which described albacore tuna as nocturnal feeders. Nonetheless, albacore tuna have been described as consuming a lower diversity of prey species (Matthews et al. 1977) and having relatively narrow trophic niches in other regions, potentially indicating specialist feeding behavior (Bertrand et al. 2002; Consoli et al. 2008; Young et al. 2010). Stable isotope analyses reinforced this hypothesis as albacore tuna was identified as having the narrowest isotopic niche width and diversity of the three predators examined.

Inter-annual fluctuations in prey importance to the diets of dolphinfish and tunas in SNE may reflect variability in large-scale ocean productivity and dolphinfish associations with shifting oceanographic features such as sea surface temperature and frontal regions (Kleisner 2009). Trends in dolphinfish ontogenetic feeding patterns observed in the SNE region have been found in other ocean basins, with dietary shifts between squid and piscine prey across seasons in the eastern Caribbean (Oxenford and Hunte 1999) and among body sizes in the eastern Pacific Ocean (Olson and Galván-Magaña 2002). Low trophic level prey such as amphipods and euphausiids, which were important primarily between 2007 and 2008, can serve as biological indicators of oceanographic

changes (Johnson et al. 2011). A weak trend of oscillation in major prey types in the diets of dolphinfish and tunas was apparent across years, with cephalopods more dominant in tuna diets in later years and the inverse for dolphinfish. Future studies including diet analysis with fine scale spatial and temporal information would improve our understanding of how meso- and top predators utilize habitats and partition prey resources.

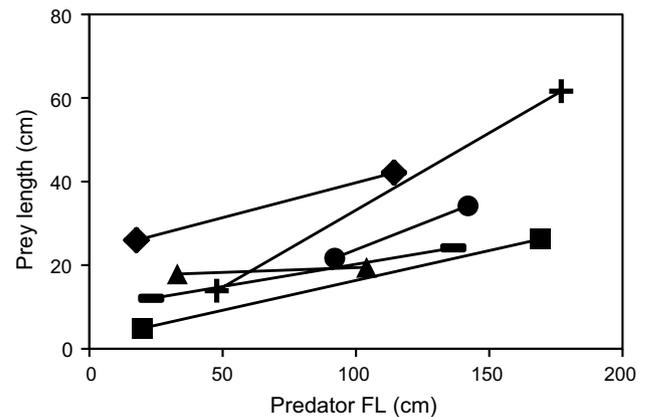
### Ontogenetic shifts in foraging habits

In the SNE region, size-based trophic niche breadths derived from prey–predator length ratio relationships showed convergence for dolphinfish and yellowfin tuna. Although sample sizes were insufficient ( $N < 40$ ) to evaluate minimum and maximum relative body size relationships between albacore tuna and their prey, average trends showed an overall decrease in relative prey size with growth. In addition, stable isotope analyses showed decreasing  $\delta^{15}\text{N}$  values with increasing predator body size in dolphinfish and no trend with yellowfin tuna ontogeny. Results suggest that dolphinfish and yellowfin tuna in the SNE region are sustained on large amounts of relatively small ( $\leq 10\%$  relative size), low trophic level prey even at large body sizes.

Greater relative prey–predator length ratios have been described for dolphinfish in the Pacific Ocean and western Mediterranean Sea (Massuti et al. 1998; Olson and Galván-Magaña 2002), though dolphinfish from SNE were smaller on average than those evaluated in other ocean basins. Since data presented here were collected from fish landed at tournaments, where the largest fish are targeted, it is uncertain whether the feeding ecology of large ( $\geq 100$  cm) dolphinfish was not adequately sampled, or that the regional population is comprised of smaller individuals. In other regions where dolphinfish diets have been evaluated, especially those that have included larger bodied individuals, maximum prey size increases with ontogeny (Fig. 9). The relatively flat relationship of maximum prey size with dolphinfish size suggests restriction of the feeding potential of dolphinfish in SNE. Variability in predator–prey body size relationships among ocean basins may also be attributable to differences in habitat types (e.g., Gulf Stream, continental shelf), prey availability (e.g., *Sargassum* presence), predator feeding behaviors, or niche segregation among other co-occurring predators, such as bigeye tuna or wahoo (Ménard et al. 2006; Young et al. 2010).

### Implications for ecosystem-based management

The high energetic demands and the prevalence of small-sized prey in tuna and dolphinfish diets indicate these predators could be contributing substantially to mortality rates of early



**Fig. 9** Maximum quantiles (95th) from studies of dolphinfish collected in the present study (filled triangle), off of North Carolina (filled square Rudershausen et al. 2010), in the eastern Caribbean Sea (solid line Oxenford and Hunte 1999), off of eastern Australia (filled circle Young et al. 2010), in the western Mediterranean Sea (filled diamond Massuti et al. 1998), and in the eastern Pacific Ocean (plus symbol Olson and Galván-Magaña 2002; Olson unpublished data). Each line is bound at the minimum and maximum length of dolphinfish evaluated by each study

life stages, impacting recruitment and the population dynamics of commercially important species such as scombrids, billfish, and ommastrephid squids. Numerous studies on a variety of large pelagic fishes have shown similar foraging trends in global oceans (Massuti et al. 1998; Olson and Galván-Magaña 2002; Pusineri et al. 2008; Ménard et al. 2006; Landsell and Young 2007; Rudershausen et al. 2010; Young et al. 2010; Staudinger et al. 2013a). This is especially important for forage populations that are also targeted by the fishing industry including the ommastrephid, shortfin squid. The size range of shortfin squid consumed by dolphinfish overlaps with those targeted by the commercial fishery ( $\geq 11$  cm; NOAA 2004), which suggests potential trade-offs for shared biomass between humans and fish predators. Estimates of total predatory demand by large pelagic predators, fishing mortality, and stock biomass remain unknown for the regional shortfin squid population (NOAA 2006). Inter-annual variation in dolphinfish dependence on shortfin squid was apparent; future studies should seek to characterize the basis for these temporal fluctuations. In addition, multispecies assessments that model size-based, annual consumption rates of shortfin squid are needed for accurate assessments of total mortality and the establishment of accurate biological reference points in the SNE region for this species (Buckel et al. 1999; Overholtz et al. 2000).

### Conclusions

To the best of our knowledge, this study presents the most northern assessment of dolphinfish food habits and trophic interactions with co-occurring yellowfin and albacore tunas

along the US Atlantic coast in the western North Atlantic (though see Logan and Lutcavage 2013, and Logan and Lutcavage 2013 in the nearby Central North Atlantic). Information gained from this study comprehensively describes the food habits of SNE dolphinfish and tunas, identifies important and shared prey as well as predator–prey length relationships, and determined the extent of dietary and isotopic niche overlap among these three predators. Our results are consistent with a study from almost four decades ago of tuna feeding habits in a nearby region (Matthews et al. 1977) that also showed yellowfin tuna associations with surface and *Sargassum* prey, and a narrower dietary niche focused on more mesopelagic prey in albacore tuna. Diets of dolphinfish contained similar prey to other regions evaluated for this predator, but with increased dependence on pelagic squids and small crustaceans in the SNE region. These baseline data will be important for future studies that seek to understand the ecological impacts of dolphinfish as their population abundance fluctuates regionally and temporally.

Shifts in marine species distributions and population sizes attributable to climate change are increasingly being documented in the western Atlantic and global marine habitats (Collie et al. 2008; Nye et al. 2009; Fodrie et al. 2010; Staudinger et al. 2013b). Poleward expansion by dolphinfish has been observed in the California Current of the Pacific Ocean and attributed to decreased coastal upwelling and resultant rising ocean temperatures (Norton 1999). Increased regional landings signify that dolphinfish population expansion may also be occurring in the western Atlantic (NOAA 2010; Whoriskey et al. 2011). Whether this increase will have a noticeable impact on shared prey resources and trophic dynamics of dolphinfish and co-occurring predators is unknown; indeed, several studies have found little evidence for dramatic climate-related shifts in predator–prey relationships among meso- and top predators in the Atlantic (e.g., Rudershausen et al. 2010) and Pacific Oceans (Griffiths et al. 2010). However, few have estimated predatory demand and consumption rates of this species on principal prey. Dolphinfish are opportunistic mesopredators, and our results demonstrate they have a wider trophic niche in the SNE region than co-occurring yellowfin and albacore tunas, which could give them a competitive advantage if resources were to shift or become scarce due to changing ecological and environmental conditions.

Predatory fishes with fast growth rates and short life spans, such as dolphinfish and yellowfin tuna, are generally more resilient to fishing pressure than those with longer life spans and slower growth rates (Schindler et al. 2002). Recent studies of dolphinfish have provided new insights into their distribution (Farrell et al. 2014), movements (Merten et al. 2014b), abundance (Kleisner 2009),

and habitat associations (Kleisner 2009) in the Atlantic Ocean and Gulf of Mexico. However, additional studies are needed to attribute population dynamics of dolphinfish in the western North Atlantic to changes in fishing, environmental conditions, or trophic interactions due to declines in competing or predatory species such as larger tunas, billfishes and sharks (Myers and Worm 2003; Polovina et al. 2009). Future research evaluating changes in the abundance and residence time of dolphinfish in the SNE region will be important to determining overall impacts of this voracious predator on principal prey populations, such as shortfin squid, that are also harvested commercially.

**Acknowledgments** We would like to thank Gregory Skomal and John Chisholm of the Massachusetts Division of Marine Fisheries for facilitating access to fishermen and fish for this project; Andy Danylchuk, John Logan and an anonymous reviewer for comments on earlier versions of this manuscript. Special thanks to the angling clubs and fishing tournament organizers who allowed us to sample at their events and their catch, especially to the crew of the Helen H Deep Sea Fishing fleet for providing valuable opportunities for sample collection. We thank Robert Murphy, Morgan Lindemayer, Nicki Jacobson, Melissa Belcher, Tyler Van Fleet, Mike Akresh, Katherine Terkanian, Sarah Martinez, Mark Teffer, Sarah Oktay and members of the UMass Boston Nantucket Field Station, as well as many others for volunteering and helping with sampling; these individuals were essential to completing this work. We thank Kim Duernberger (University of North Carolina Wilmington) for her help with stable isotope analysis and Mike Vecchione and Richard Young for their help identifying cephalopod specimens and beaks. Thanks to Hazel Oxenford for supplying raw data valuable to this manuscript. Funding for this project was provided by a Massachusetts Agricultural Research Station Hatch Grant, the University of Massachusetts School of Marine Sciences, and the Center for Marine Science at the University of North Carolina Wilmington.

## References

- Allain V, Fernandez E, Hoyle SD, Caillot S, Jurado-Molina J, Andreouet S, Nicol SJ (2012) Interaction between coastal and oceanic ecosystems of the western and central Pacific Ocean through predator-prey relationship studies. *PLoS ONE* 7(5):e36701
- Baque-Menoscal J, Páez-Rosas D, Wolff M (2012) Feeding habits of two pelagic fish *Thunnus albacares* and *Acanthocybium solandri* from the Galapagos Marine Reserve. *Rev Biol Mar Oceanogr* 47:1–11
- Bertrand A, Bard FX, Josse E (2002) Tuna food habits related to the micronekton distribution in French Polynesia. *Mar Biol* 140:1023–1037
- Buckel JA, Conover DO, Steinberg ND, McKown KA (1999) Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (*Morone saxatilis*). *Can J Fish Aquat Sci* 56:275–287
- Butler CM, Logan JM, Provaznik JM, Hoffmayer ER, Staudinger MD, Quattro JM, Roberts MA, Ingram GW, Pollack AG, Lutcavage ME (2015) Atlantic bluefin tuna (*Thunnus thynnus*) feeding ecology in the northern Gulf of Mexico: a preliminary description of diets from the western Atlantic spawning grounds. *J Fish Biol* 86:365–374

- Casazza TL, Ross SW (2008) Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. *Fish Bull* 106:348–363
- Castro JJ, Santiago JA, Hernandez-Garcia V, Pla C (1999) Growth and reproduction of the dolphinfish (*Coryphaena equiselis* and *Coryphaena hippurus*) in the Canary Islands, Central-East Atlantic (preliminary results). *Sci Mar* 63:317–325
- Chase BC (2002) Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. *Fish Bull* 100:168–180
- Chaudhuri AH, Bisagni JJ, Gangopadhyay A (2009) Shelf water entrainment by Gulf Stream warm-core rings between 751 W and 501 W during 1978–1999. *Cont Shelf Res* 29:393–406
- Chouvelon T, Spitz J, Caurant F, Méndez-Fernandez P, Chappuis A, Laugier F, Le Goff E, Bustamante P (2012) Revisiting the use of  $\delta^{15}\text{N}$  in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures—the case of an open ecosystem: the Bay of Biscay (North-East Atlantic). *Prog Oceanogr* 101:92–105
- Clarke MR (1996) The role of cephalopods in the world's oceans: an introduction. *Philos Trans R Soc B* 351:979–983
- Collie JS, Wood AD, Jeffries HP (2008) Long-term shifts in the species composition of a coastal fish community. *Can J Fish Aquat Sci* 65:1352–1365
- Consoli P, Romeo T, Battaglia P, Castriota L, Esposito V, Andaloro F (2008) Feeding habits of the albacore tuna *Thunnus alalunga* (Perciformes, Scombridae) from the central Mediterranean Sea. *Mar Biol* 155:113–120
- Cook AM, Bundy A (2011) The food habits database: an update, determination of sampling adequacy and estimation of diet for key species. Canadian technical report of fisheries and aquatic sciences, vol 2884, 144 pp
- Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can J Fish Aquat Sci* 54:726–738
- Cosgrove R, Arregui I, Arrizabalaga H, Goñi N, Sheridan M (2014) New insights to behaviour of North Atlantic albacore tuna (*Thunnus alalunga*) observed with pop-up satellite archival tags. *Fish Res* 150:89–99
- Dagorn L, Holland KN, Hallier J, Taquet M, Moreno G, Sancho G, Fonteneau A et al (2006) Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). *Aquat Living Resour* 19:85–88
- Estrada JA, Luttcavage M, Thorrold SR (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. *Mar Biol* 147:37–45
- Farrell ER, Boustany AM, Halpin PN, Hammond DL (2014) Dolphinfish (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic. *Fish Res* 151:177–190
- Fodrie FJ, Heck KL Jr, Powers SP, Graham WM, Robinson KL (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Glob Change Biol* 16:48–59
- Fry B (2006) Stable isotope ecology. Springer, New York
- Galli GLJ, Shiels HA, Brill RW (2009) Temperature sensitivity of cardiac function in pelagic fishes with different mobilities: yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), mahimahi (*Coryphaena hippurus*), and swordfish (*Xiphias gladius*). *Physiol Biochem Zool* 82:280–290
- Gibbs RH, Collette BB (1959) On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. *Bull Mar Sci Gulf Caribb* 9:117–152
- Golet WJ, Cooper AB, Campbell R, Luttcavage M (2007) Decline in condition of northern bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine. *Fish Bull* 105:390–395
- Goñi N, Logan J, Arrizabalaga H, Jarry M, Luttcavage M (2011) Variability of albacore (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea. *Mar Biol* 158:1057–1073
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Graham BS (2008) Trophic dynamics and movements of tuna in the Tropical Pacific Ocean inferred from stable isotope analyses. Ph.D. Thesis, University of Hawaii, Manoa, Hawaii, USA
- Griffiths SP, Young JW, Lansdell MJ, Campbell RA, Hampton J, Hoyle SD, Langley A, Bromhead D, Hinton MG (2010) Ecological effects of longline fishing and climate change on the pelagic ecosystem off eastern Australia. *Rev Fish Biol Fish* 20:239–272
- International Commission for the Conservation of Atlantic Tunas (ICCAT) (2010) Stock assessment and fishery evaluation (SAFE) report for Atlantic highly migratory species. [http://www.nmfs.noaa.gov/sfa/hms/Safe\\_Report/2010/HMS\\_SAFE\\_Report\\_2010\\_FINAL\\_FULL\\_DOCUMENT.pdf](http://www.nmfs.noaa.gov/sfa/hms/Safe_Report/2010/HMS_SAFE_Report_2010_FINAL_FULL_DOCUMENT.pdf). Accessed 28 Sep 2011
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE* 7(2):e31757
- Johnson CL, Runge JA, Curtis KA, Durbin EG, Hare JA, Incze LS, Link JS, Melvin GD, O'Brien TD, Van Guelpen L (2011) Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. *PLoS ONE* 6:e16491
- Juanes F (2003) The allometry of cannibalism in piscivorous fishes. *Can J Fish Aquat Sci* 60:594–602
- Kitchell JF, Boggs CH, He X, Walters CJ (1999) Keystone predators in the Central Pacific. In: Ecosystem approaches for fisheries management. Alaska Sea Grant Program, AL-SG-99-01, Fairbanks, 756 pp
- Kitchell JF, Essington TE, Boggs CH, Schindler DE, Walters CJ (2002) The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. *Ecosystems* 5:202–216
- Kleisner KM (2009) A spatio-temporal analysis of dolphinfish, *Coryphaena hippurus*, abundance in the Western Atlantic: implications for stock assessment of a data-limited pelagic resource. Dissertation, University of Miami, Miami, FL, USA
- Kleisner KM, Walter JF III, Diamond SL, Die DJ (2010) Modeling the spatial autocorrelation of pelagic fish abundance. *Mar Ecol Prog Ser* 411:203–213
- Kline TC Jr (2002) Relative trophic position of *Cancer magister* megalopae. In: Paul AJ, Dawe EG, Elnor R, Jamieson GS, Kruse GH, Otto RS, Sainte-Marie B, Shirley TC, Woodby D (eds) Crabs in cold water regions: biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, pp 645–649
- Koenker R (2012) quantreg: quantile regression. R package version 4.78, <http://CRAN.R-project.org/package=quantreg>. Accessed 28 Sep 2011
- Landsell M, Young J (2007) Pelagic cephalopods from eastern Australia: species composition, horizontal and vertical distribution determined from the diets of pelagic fishes. *Rev Fish Biol Fish* 17:125–138

- Layman CA, Arrington DA, Montana CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Levitus S, Antonov J, Boyer T, Stephens C (2000) Warming of the world ocean. *Science* 287:2225–2229
- Link JS (2004) Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. *Mar Ecol Prog Ser* 269:265–275
- Logan JM, Lutcavage ME (2013) Assessment of trophic dynamics of cephalopods and large pelagic fishes in the central North Atlantic Ocean using stable isotope analysis. *DSR II* 95:63–73
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modeling methods. *J Anim Ecol* 77(4):838–846
- Logan JM, Rodriguez-Marin E, Goñi N, Barreiro S, Arrizabalaga H, Golet W, Lutcavage ME (2011) Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Mar Biol* 158:73–85
- Logan JM, Golet WJ, Lutcavage ME (2015) Diet and condition of Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine, 2004–2008. *Environ Biol Fish* 98:1411–1430
- Macdonald JS, Green RH (1983) Redundancy of variables used to describe importance of prey species in fish diets. *Can J Fish Aquat Sci* 40:635–637
- MacNeil MA, Drouillard KG, Fisk A (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. *Mar Ecol Prog Ser* 302:199–206
- Madigan DJ, Litvin SY, Popp BN, Carlisle AB, Farwell CJ, Block BA (2012) Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific bluefin tuna (*Thunnus orientalis*). *PLoS ONE* 7:e49220
- Magnuson JJ, Heitz JG (1971) Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fish Bull* 69:361–370
- Massuti E, Deudero S, Sánchez P, Morales-Nin B (1998) Diet and feeding of dolphin (*Coryphaena hippurus* L.) in western Mediterranean waters. *Bull Mar Sci* 63:329–341
- Matthews FD, Damkaer DM, Knapp LW, Collette BB (1977) Food of western North Atlantic Tunas (*Thunnus*) and Lancetfishes (*Alepisaurus*). NOAA technical report NMCS SSRF-706, 19 pp
- Ménard F, Labruno C, Shin Y, Asine A, Bard F (2006) Opportunistic predation in tuna: a size-based approach. *Mar Ecol Prog Ser* 323:223–231
- Merten W, Appeldoorn R, Rivera R, Hammond D (2014a) Diel vertical movements of adult male dolphinfish (*Coryphaena hippurus*) in the western central Atlantic as determined by use of pop-up satellite archival transmitters. *Mar Biol* 161:1823–1834
- Merten W, Appeldoorn R, Hammond D (2014b) Movements of dolphinfish (*Coryphaena hippurus*) along the U.S. east coast as determined through mark and recapture data. *Fish Res* 151:114–121
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- National Marine Fisheries Service (NMFS) (2006) 42nd northeast regional stock assessment workshop (42nd SAW): 42nd SAW assessment summary report. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 06-01, 61 pp
- Naval Research Laboratory Global Ocean Analysis and Modeling (2011) SST Nowcast. [http://www7320.nrlssc.navy.mil/global\\_nlom32/gfs.html](http://www7320.nrlssc.navy.mil/global_nlom32/gfs.html). Accessed 28 Sep 2011
- NOAA Northeast Fishery Science Center (2004) Essential fish habitat source document: northern shortfin squid, *Illex illecebrosus*, life history and habitat characteristics second edition. Retrieved on May 1, 2012 from <http://www.nefsc.noaa.gov/publications/tm/tm191/tm191.pdf>
- NOAA Northeast Fishery Science Center (2010) Annual landings query. [http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). Accessed 27 July 2013
- Norton JG (1999) Apparent habitat extensions of dolphinfish (*Coryphaena hippurus*) in response to climate transients in the California Current. *Sci Mar* 63:239–260
- Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar Ecol Prog Ser* 393:111–129
- Olson RJ, Galván-Magaña F (2002) Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fish Bull* 100:279–298
- Olson RJ, Popp BN, Graham BS, López-Ibarra GA, Galván-Magaña F, Lennert-Cody CE, Bocanegra-Castillo N, Wallsgrove NJ, Gier E, Alatorre-Ramírez V, Balance LT, Fry B (2010) Food-web inferences of stable isotope spatial patterns in copepods and yellowfin tuna in the pelagic eastern Pacific Ocean. *Prog Oceanogr* 86:124–138
- Overholtz WJ (2006) Estimates of consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) during 1970–2002: an approach incorporating uncertainty. *J Northwest Atl Fish Sci* 36:55–63
- Overholtz WJ, Link JS, Suslowicz LE (2000) Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES J Mar Sci* 57:1147–1159
- Oxenford HA (1999) Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review. *Sci Mar* 63:277–301
- Oxenford HA, Hunte W (1999) Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Sci Mar* 63:305–315
- Palko BJ, Beardsley GL, Rickards WJ (1982) Synopsis of the biological data on dolphin fishes *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. NOAA technical report NMFS circular 443, 28 pp
- Parisi-Baradad V, Manjabacas A, Lombarte A, Olivella R, Chic O, Piera J, Garcia-Ladona E (2010) Automated Taxon Identification of Teleost fishes using an otolith online database—AFORO. *Fish Res* 105:13–20
- Parnell A, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672
- Pinkas L, Oliphant S, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif Dep Fish Game Fish Bull* 152:1–105
- Polovina JJ, Abecassis M, Howell EA, Woodworth P (2009) Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996–2006. *Fish Bull* 107:523–531
- Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, López-Ibarra G, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable isotopes as indicators of ecological change. Elsevier Academic Press, Burlington, MA, pp 173–190
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Pusineri C, Chancollon O, Ringelstein J, Ridoux V (2008) Feeding niche segregation among the northeast Atlantic community of oceanic top predators. *Mar Ecol Prog Ser* 361:21–34
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>

- Rayner NA, Brohan P, Parker DE, Folland CK, Kennedy JJ, Vanicek M, Ansell TJ, Tett SFB (2006) Improved analyses of changes and uncertainties in sea surface temperature measured in situ since the mid-nineteenth century: the HadSST2 dataset. *J Clim* 19:446–469
- Robins CR, Ray GC, Douglass J (1986) A field guide to Atlantic Coast fishes of North America. The Peterson Guide Series, vol 32. Houghton Mifflin Company, Massachusetts
- Rogers WH (1992) Quantile regression standard errors. *Stata Tech Bull* 9:16–19
- Rose CD, Hassler WW (1974) Food habits and sex ratios of dolphin *Coryphaena hippurus* captured in the western Atlantic Ocean off Hatteras, North Carolina. *Trans Am Fish Soc* 103:94–100
- Rountree RA (1990) Community structure of fishes attracted to shallow water fish aggregation devices off South Carolina USA. *Environ Biol Fish* 29:241–262
- Rudershausen PJ, Buckel JA, Edwards J, Gannon DP, Butler CM, Averett TW (2010) Feeding ecology of blue marlins, dolphinfish, yellowfin tuna, and wahoos from the North Atlantic Ocean and comparisons with other oceans. *Trans Am Fish Soc* 139:1335–1359
- Santos MB, Clarke MR, Pierce GJ (2001) Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fish Res* 52:121–139
- Scharf FS, Yetter RM, Summers AP, Juanes F (1998a) Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains. *Fish Bull* 96:575–588
- Scharf F, Juanes F, Sutherland M (1998b) Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460
- Scharf F, Juanes F, Rountree R (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Schindler DE, Essington TE, Kitchell JF, Boggs C, Hilborn R (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecol Appl* 12:735–748
- Schoener TW (1974) Some methods for calculating competition coefficients from resource utilization spectra. *Am Nat* 108:332–340
- Schwenke KL, Buckel JA (2008) Age, growth, and reproduction of dolphinfish (*Coryphaena hippurus*) caught off the coast of North Carolina. *Fish Bull* 106:82–92
- Staudinger MD, Juanes F, Carlson S (2009) Reconstruction of original body size and estimation of allometric relationships for the longfin inshore squid (*Loligo pealeii*) and northern shortfin squid (*Illex illecebrosus*). *Fish Bull* 107:101–105
- Staudinger MD, Juanes F, Salmon B, Teffer AK (2013a) The distribution, diversity and importance of cephalopods in top predator diets from offshore habitats of the Northwest Atlantic Ocean. *Deep Sea Res Pt II* 95:185–195
- Staudinger MD, Carter S, Cross M, Dubois N, Duffy E, Enquist C, Griffis R, Hellmann J, Lawler J, Morrison S, O’Leary J, Stein B, Turner W (2013b) Biodiversity in a changing climate: a synthesis of current and projected trends in the United States. *Front Ecol Environ* 11:465–473
- Staudinger MD, McLarny RJ, McLellan WA, Pabst DA (2014) Foraging ecology and niche overlap in pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales from waters of the U.S. mid-Atlantic coast. *Mar Mamm Sci* 30:626–655
- Teffer AK, Staudinger MD, Taylor DL, Juanes F (2014) Trophic influences on mercury accumulation in top pelagic predators from offshore New England waters of the northwest Atlantic Ocean. *Mar Environ Res* 101:124–134
- Thompson NB (1999) Characterization of the dolphinfish (*Coryphaenidae*) fishery of the United States western north Atlantic Ocean. *Sci Mar* 63:421–427
- Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* 86:835–847
- Whoriskey S, Arauz R, Baum JK (2011) Potential impacts of emerging mahi-mahi fisheries on sea turtle and elasmobranch bycatch species. *Biol Conserv* 144:1841–1849
- Young JW, Lansdell MJ, Campbell RA, Cooper SP, Juanes F, Guest MA (2010) Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar Biol* 157:2347–2368