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The distribution, diversity, and importance of cephalopods in top predator diets from offshore habitats of the Northwest Atlantic Ocean



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ABSTRACT

Large pelagic predators were used as biological samplers to gain information on cephalopod diversity, abundance, distribution, and their role as prey in the Northwest Atlantic Ocean. Fish predators were caught by recreational anglers in offshore waters of New England (NE; 2007–2010), the Mid-Atlantic Bight (MAB; 2009–2010) and the South Atlantic Bight (SAB; 2010–2011). In total, 2362 cephalopods, including 22 species of squid and 4 octopods, were identified in the diets of 13 species of predatory fishes. Cephalopod body sizes were obtained for 1973 specimens through direct measurement of mantle lengths (ML) or estimated using lower rostral/hood lengths of lower beaks. Cephalopod diversity (number of species) was highest in predator diets from the SAB ($N=19$), intermediate in NE ($N=18$), and lowest in the MAB ($N=9$); however, differences may reflect unequal sampling effort among regions. The most important cephalopods across predator diets by number and frequency of occurrence were from the families Ommastrephidae, Argonautidae, Loliginidae, and Histioteuthidae. Shortfin squid (*Illex illecebrosus*) and paper nautilus (*Argonauta* sp.) were the most recurrent species identified across spatiotemporal scales; size distributions of these two species varied significantly among regions, and the largest individuals on average were found in the MAB. Results demonstrate that although pelagic predators consumed a broad range of cephalopod species, octopods and squids from the families Argonautidae and Ommastrephidae dominated the collective diets of numerous pelagic teleosts and elasmobranchs, and play a key role in offshore food-webs of the Northwest Atlantic Ocean. This study emphasizes the value of using predators as biological samplers to gain information on cephalopod biogeography, and as a potential approach to track ecosystem changes in this region due to environmental and anthropogenic stressors.

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1. Introduction

Global marine biodiversity and ecosystems face a growing threat from anthropogenic stressors including exploitation and climate change; consequently, there is an increasing need for baseline information on the abundance and distribution of marine populations, as well as improved descriptions of species trophic roles (Block et al., 2011; Cheung et al., 2009; Nye et al., 2010; Tittensor et al., 2010; Zeidberg and Robison, 2007). Cephalopods are important components of marine food-webs, serving as predators and competitors to fishes and crustaceans, as well as prey to a wide range of finfishes, sharks, toothed whales, and pinnipeds (Clarke, 1996; Overholtz et al., 2000; Pierotti, 1988;

Staudinger and Juanes, 2010a). It is widely believed that during the past several decades, cephalopod populations have increased globally as their finfish and elasmobranch predators and competitors have declined due to overexploitation (Caddy and Rodhouse, 1998); the direct and indirect effects of predator and cephalopod population shifts on ecosystem structure and function are largely unknown, especially in offshore communities where data on cephalopod biogeography and ecology are scarce (Cherel et al., 2004; Rodhouse and White, 1995; Vecchione and Galbraith, 2001).

Cephalopods, predominantly gelatinous and large species that reside in offshore environments, are difficult to capture by fishing gears (e.g., trawls and nets), thus traditional surveys have yielded little information on these species. In contrast, teuthophagous predators consume a greater diversity of species and a wider size-range of cephalopods than are caught by most sampling gears (Cherel et al., 2004; Clarke, 2006, 1980). Because cephalopod

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beaks accumulate in the stomachs of many top predators, beaks obtained from predator diets offer an alternative approach to gain information on cephalopod diversity, distribution, and importance in regional ecosystems (Cherel et al., 2007, 2004; Clarke, 2006, 1980).

The primary goals of this study were to (1) provide baseline information on the role of cephalopods as prey in offshore food-webs of the Northwest Atlantic Ocean, and (2) examine cephalopod diversity, relative abundance, and distribution over temporal and spatial scales using apex predators as biological samplers. A better understanding of species relationships and functional roles within regional communities is critical for ecosystem-based management of cephalopods and their predators, particularly those that are exploited commercially (e.g., Loliginidae and Ommastrephidae).

2. Methods

Stomach contents were collected from a variety of finfish and elasmobranch predators along the US Atlantic coast between August 2007–July 2011 (Table 1). Fishes landed at recreational sportfishing tournaments, charter boat centers, and commercial fishing ports were sampled in New England (NE) between July and September during 2007–2010, the Mid-Atlantic Bight (MAB) during August 2009 and 2010, and in the South Atlantic Bight (SAB) between March 2010 and July 2011. Fishes were primarily caught by anglers trolling ballyhoo (*Hemiramphus brasiliensis*) bait and artificial lures in waters over the continental shelf break and slope as well as in the Gulf Stream Current. Fishing occurred during the daytime generally between the hours of 0900 and 1500 h, and boats fished in waters that they could reach and return from as day-trips from marinas and ports along the coasts of Massachusetts, New Jersey, North Carolina, and South Carolina. After fishes were transported back to the docks on ice by fishers, body sizes of scombrids, sharks, and dolphinfish (*Coryphaena*

hippurus) were measured as fork length (FL) in centimeters (cm), and billfishes as lower jaw fork length (LJFL); stomachs were removed, placed on ice, transported to the laboratory, and frozen until the time of analysis.

In the laboratory, stomachs were thawed, prey items were sorted into broad taxonomic categories (cephalopod, fish, crustacean, other), weighed to the nearest gram (g), counted, and mantle lengths (ML) were measured directly in cm when specimens were intact and relatively undigested. Lower and upper beaks were used to identify cephalopods to the level of species or family using reference guides (Clarke, 1986; Lu and Ickeringill, 2002; Xavier and Cherel, 2009), comparison with collections at the National Museum of Natural History (NMNH), and our own reference collection. Lower rostral lengths (LRL) and lower hood lengths (LHL) of lower beaks from teuthoids and octopods, respectively, were measured in millimeters (mm) using digital calipers, and predictive equations were used to reconstruct cephalopod ML from previously published equations (Table 2) (Clarke, 1986; Lu and Ickeringill, 2002; Staudinger et al., 2009; Xavier and Cherel, 2009).

Allometric equations were developed for several species that were not reported in the literature using measurements from intact specimens recovered from predator diets (*Argonauta* sp.), collections at the National Museum of Natural History (NMNH) (*Illex illecebrosus*), and collected as part of the National Marine Fisheries Service (Northeast Fisheries Science Center) bottom trawl survey (Sepiolidae and *Abralia veranyi*) (Azarovitz, 1981). Least-squares regressions were used to evaluate the relationships between LRL or LHL, ML (mm) and mass (g). Data were log₁₀ transformed prior to use in parametric analyses to meet the assumptions of normality and homogeneity of variance (Sokal and Rohlf, 1995). Equations were then used to estimate ML and mass (g) in these species (Table 2).

The total contribution of all cephalopods to predator diets was calculated as percent mass (%M), percent by number (%N), and percent frequency of occurrence relative to other prey categories

Table 1

Predator species and body sizes caught in waters off of New England (NE), the Mid-Atlantic Bight (MAB), and the South Atlantic Bight (SAB) between 2007 and 2011. Prey diversity indicates the number of cephalopod species found in each predator's diet.

Predator species		Number of predators sampled per region			Number of stomachs with cephalopod prey	Prey diversity	Mean predator length ± SD (cm)	
		NE	MAB	SAB				
Coryphaenidae								
Dolphinfish	<i>Coryphaena hippurus</i>	115	4	174	83	11	82.2	± 20.90
Scombridae								
Albacore tuna	<i>Thunnus alalunga</i>	23	–	–	18	5	96.1	± 12.13
Bigeye tuna	<i>Thunnus obesus</i>	2	1	1	4	5	169.0	± 10.41
Blackfin tuna	<i>Thunnus atlanticus</i>	–	–	91	47	12	70.4	± 13.32
Yellowfin tuna	<i>Thunnus albacores</i>	83	14	13	84	13	108.1	± 16.43
Wahoo	<i>Acanthocybium solanderi</i>	14	4	86	20	8	130.8	± 20.71
Istiophoridae								
Roundscale spearfish	<i>Tetrapturus georgii</i>	–	9	–	6	4	177.8	± 5.88
White marlin	<i>Tetrapturus albidus</i>	–	20	–	13	3	173.4	± 4.76
Blue marlin	<i>Makaira nigricans</i>	–	4	1	0	0	269.5	± 5.93
Xiphiidae								
Swordfish	<i>Xiphias gladius</i>	3	–	–	3	7	142.9	± 9.22
Elasmobranchii								
Porbeagle shark	<i>Lamna nasus</i>	3	–	–	2	2	216.2	± 2.75
Shortfin mako shark	<i>Isurus oxyrinchus</i>	29	–	1	9	2	197.9	± 21.83
Thresher shark	<i>Alopias vulpinus</i>	33	–	–	5	2	207.3	± 24.13

Table 2
Predictive equations for reconstructing dorsal mantle length (ML) and body mass (g) from lower hood lengths (HL) in octopods and lower rostral lengths (LRL) in decapods. All length measurements are in millimeters (mm).

Species	Equation	N	F	R ²	p
Argonautidae					
<i>Argonauta</i> sp.	ln ML = 1.314 × ln LHL + 2.272	8	123.6	0.96	< 0.0001
	ln Mass = 3.455 × ln LHL - 1.504	9	21.4	0.75	0.0024
Enoploteuthidae					
<i>Abralia veranyi</i>	ln ML = 0.537 × ln LRL + 3.411	29	19.2	0.42	0.0002
	ln Mass = 1.968 × ln LRL + 0.362	29	33.5	0.55	< 0.0001
Ommastrephidae					
<i>Illex illecebrosus</i> ^a	ln ML = 1.105 × ln LRL + 4.071	93	1612.2	0.95	< 0.0001
Sepiolidae					
	ln ML = 0.724 × ln LRL + 3.242	52	31.4	0.39	< 0.0001
	ln Mass = 2.118 × ln LRL + 1.625	52	54.8	0.52	< 0.0001

^a Equation has been updated with information from an expanded size range of specimens from Staudinger et al. (2009).

across the stomachs of each predator (%FO). An index of relative importance (%IRI) was calculated as %FO (%N + %M) (Cortés, 1997; Pinkas et al., 1971).

Frequency of occurrence was chosen to assess the relative abundance of cephalopods in Northwest Atlantic waters because it is subject to less bias than other diet metrics (e.g., mass or number), and reflects how often predators encountered a particular prey in the environment based on the relative number of stomachs examined (Fahrig et al., 1993; Link, 2004); however, this method is limited in that it assumes no selectivity by predators. Frequency of occurrence was assessed for each cephalopod family found across all predator stomachs sampled in each region and seasonal period. Seasonal time periods were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

Differences in mean prey body sizes consumed by predators were compared with one-way ANOVA models, and minimum significant differences were compared using the Tukey–Kramer method (Sokal and Rohlf, 1995). The Kruskal–Wallis test, which is the non-parametric equivalent of a one-way ANOVA, was chosen to evaluate differences in cephalopod body sizes among regions since distributions were found to violate assumptions of normality (Zar, 1984).

3. Results

3.1. Species diversity and relative abundance

The remains of 2362 cephalopods were recovered from 728 stomachs of 13 species of finfish and elasmobranch predators. In total, 26 species of cephalopods, including 22 squids and 4 octopods, were identified in predator diets (Table 3). Cephalopod diversity (number of species) was slightly greater in the SAB (N = 19) compared to NE (N = 18), and twice as high in comparison to the MAB (N = 9); however, sampling effort varied among predators and seasons in each region and likely affected the number of cephalopod species found. Overall, the number of cephalopod species found in each region increased with the total number of stomachs sampled, and dolphinfish, blackfin (*Thunnus atlanticus*) and yellowfin (*Thunnus albacores*) tunas consumed the greatest diversity of cephalopods of all predators examined (Table 1).

Families present across all regions included Enoploteuthidae, Histioteuthidae, Loliginidae, Ommastrephidae, Sepiolidae, and Argonautidae. In contrast, Ancistrocheiridae, Brachioteuthidae, Mastigoteuthidae, the two cranchiids, *Galiteuthis armata*, and *Teuthowenia megalops*, and young benthic octopods were found

only in NE waters; Lepidoteuthidae, Onychoteuthidae, and the cranchiid, *Cranchia scabra*, were only observed in the SAB (Fig. 1).

Regional and seasonal comparisons revealed the highest diversity of cephalopod families were present in predator diets during summer in NE, and spring in the SAB (Fig. 1). Ommastrephids exhibited the highest frequency of occurrence of all cephalopod taxa across regions and seasons, and were relatively more abundant during fall in NE (43.6% FO), and winter in the SAB (41.4% FO). The relative abundance of argonauts in the MAB (23.0% FO) was three to four times higher than in NE (6.2% FO) and the SAB (8.7% FO) during summer, and showed an overall maximum during winter in the SAB (24.1% FO). Maximum abundances were observed for Histioteuthidae in the MAB during summer (6.6% FO), and for Loliginidae (10.4% FO), Lepidoteuthidae (10.4% FO), Sepiolidae (6.9% FO), Cranchiidae (3.5% FO) and Enoploteuthidae (3.5% FO) in the SAB during winter (Fig. 1).

3.2. Cephalopods role as prey

The five most important cephalopod families by number and frequency of occurrence consumed across all predators were Ommastrephidae, Argonautidae, Loliginidae, Enoploteuthidae, and Histioteuthidae (Table 3; Fig. 1). Shortfin squid (*I. illecebrosus*) and paper nautilus (*Argonauta* sp.) were the most recurrent species of squid and octopod, respectively, across all seasons and regions sampled during this study (Table 3). *I. illecebrosus* were present in the diets of all predators examined except mako sharks (*Isurus oxyrinchus*), and *Argonauta* sp. were consumed by a range of predators known to forage in the epipelagic zone including dolphinfish, wahoo (*Acanthocybium solanderi*), albacore (*Thunnus alalunga*), blackfin, and yellowfin tunas, as well as the two istiophorids, roundscale spearfish (*Tetrapturus georgii*), and white marlin (*Tetrapturus albidus*).

Other relatively important prey species included *Histioteuthis reversa* and *H. bonnellii*, which were eaten by wahoo, yellowfin tuna, roundscale spearfish, and dolphinfish during summer and early fall. *Abralia* sp. was not common across predator species and regions; however, 53 individuals were recovered from a single yellowfin tuna landed in NE waters during fall of 2007. Several additional enoploteuthids were retrieved from the diets of bigeye (*Thunnus obesus*), blackfin, and yellowfin tunas. Other species of note that occurred less frequently included a specimen of *Ancistroteuthis lichtensteinii*, which was found in the stomach of a mako shark in NE waters during summer. Several specimens of *Chiroteuthis veranyi* were recovered from swordfish (*Xiphias gladius*), bigeye tuna, and dolphinfish diets in NE and SAB during summer, and swordfish stomachs contained several individuals from the family Brachioteuthidae, and Cranchiidae. Lastly, several

Table 3

Total number of cephalopods (N), and frequency of occurrence (FO) of species across all stomachs sampled between 2007 and 2011 in northwest Atlantic waters. Lower rostral and hood lengths (LRL, LHL) were measured directly; mantle lengths (ML) were measured directly or reconstructed using published equations from Clarke (1986), Lu and Ickeringill (2002), Staudinger et al. (2009), Xavier and Cherel (2009), and Eqs. in Table 2.

Species	N	FO	Mean LRL/ LHL (mm) ± SD	Range	Mean ML (cm) ± SD	Range
Decapoda						
Ancistrocheiridae						
<i>Ancistrocheirus lichtensteini</i>	1	1	4.52	–	14.29	–
Brachioteuthidae						
<i>Brachioteuthis</i> sp.	3	1	2.17 ± 0.08	2.10–2.25	6.02 ± 0.15	5.87–6.17
Chiroteuthidae						
<i>Chiroteuthis veranyi</i>	5	4	3.65 ± 1.45	1.35–5.28	10.06 ± 3.54	4.44–14.05
Cranchiidae						
<i>Cranchia scabra</i>	2	2	0.63 ± 0.19	0.49–0.76	4.83 ± 0.93	4.17–5.48
<i>Galiteuthis armata</i>	1	1	3.73	–	16.43	–
<i>Teuthowenia megalops</i>	3	1	4.56 ± 1.05	3.35–5.26	19.80 ± 4.28	14.88–22.67
Cranchiidae uncl. ^a	1	1	3.28	–	17.76	–
Enoploteuthidae						
<i>Abralia veranyi</i>	57	4	1.27 ± 0.19	0.94–1.66	3.05 ± 0.42	2.30–3.97
<i>Abralia</i> sp.	2	1	0.98 ± 0.02	0.96–0.99	3.02 ± 0.03	3.00–3.04
<i>Enoploteuthis</i> sp.	2	2	1.05 ± 0.57	0.65–1.45	3.13 ± 0.81	2.56–3.70
Histioteuthidae						
<i>Histioteuthis bonnellii</i>	3	3	5.67 ± 0.45	5.15–6.00	11.23 ± 1.01	10.08–11.63
<i>Histioteuthis reversa</i>	11	8	2.37 ± 0.24	1.88–2.56	7.04 ± 6.37	2.82–18.50
<i>Histioteuthis</i> uncl. ^a	1	1	–	–	–	–
Lepidoteuthidae	9	4	1.13 ± 0.21	0.85–1.40	3.92 ± 1.05	1.81–5.07
Loliginidae						
<i>Doryteuthis pealeii</i>	69	29	1.37 ± 0.68	0.41–3.47	11.25 ± 5.94	0.83–31.81
Mastigoteuthidae						
<i>Mastigoteuthis</i> uncl. A	1	1	1.48	–	4.12	–
<i>Mastigoteuthis</i> uncl. B	1	1	1.12	–	3.08	–
Ommastrephidae						
<i>Illex illecebrosus</i>	1181	176	1.99 ± 1.03	0.25–4.52	10.49 ± 5.05	1.31–28.46
<i>Ornithoteuthis antillarum</i>	50	18	1.54 ± 0.55	0.58–3.21	4.25 ± 2.12	0.56–10.76
Unclassified ^{b,a}	61	26	1.07 ± 0.41	0.18–2.50	5.32 ± 1.99	0.96–12.31
Onychoteuthis						
<i>Onychoteuthis banksii</i>	7	6	1.02 ± 0.27	0.78–1.55	3.32 ± 1.67	1.87–6.57
<i>Onychoteuthis</i> uncl.	1	1	2.20	–	4.72	–
Sepiolidae						
<i>Rossia molleri</i>	8	7	0.61 ± 0.26	0.30–1.04	2.68 ± 0.53	1.62–3.27
Sepiolid uncl. ^c	6	5	0.95 ± 0.37	0.47–1.49	2.43 ± 0.69	1.48–3.41
Octopodiformes						
Argonautidae						
<i>Argonauta argo</i>	95	63	2.50 ± 1.13	0.54–6.57	3.48 ± 2.14	0.43–11.50
Alloposidae						
<i>Haliphron atlanticus</i>	4	4	14.05 ± 1.23	13.18–14.92	–	–
Octopodidae						
<i>Macrotritopus defilippi</i> ^a	1	1	–	–	1.50	–
Octopodidae uncl. ^a	8	7	–	–	2.32 ± 3.63	0.50–8.80
Cephalopoda unclassified^b	768	139	1.85 ± 1.08	0.15–3.98	5.29 ± 2.60	3.00–14.0
Total	2362					

^a Lower beaks were either broken or too small to measure.

^b Upper beaks, pens, eye lenses, or tissue were found.

^c Beaks could not be identified to the level of species, but morphological differences suggest more than one species were present.

species of sepiolids, including *Rossia molleri* were consumed by tunas across all regions during summer and early fall (Fig. 1).

Cephalopods were most important to the diets of bigeye tuna, swordfish, and porbeagle sharks (*Lamna nasus*) (Table 4); however, relatively few individuals of each of these predators were sampled overall, thus it is likely that cephalopods were overrepresented in the diets of these species and should be viewed as preliminary (Table 1). Regional comparisons of predator diets revealed cephalopods were more important to dolphinfish in NE waters (%IRI=29.8%), than in SAB (%IRI=4.5%) and MAB (%IRI < 1.0%). Yellowfin tuna diets varied by %N and %M across all regions, but %IRI was nearly equal in NE (33.7%) and SAB (33.3%) waters, and moderately less in the MAB (19.3%). Cephalopods were most important to wahoo diets in the MAB (%IRI=46.1%); however, the fewest number of wahoo were sampled in this region. In general, the cephalopod component of tuna diets was higher by %N than %M in the SAB compared to NE

and MAB. Roundscale spearfish and white marlin diets, which were only sampled in the MAB during August, also contained greater numbers (%N=25.5–53.5%) of cephalopods than biomass (%M=12.8–21.1%) (Table 4).

3.3. Cephalopod size distributions

Body size measurements were obtained for 1973 specimens either through direct measurement of mantle lengths or by reconstructing body sizes from the lower rostral and hood lengths of lower beaks. The largest cephalopods overall, *Doryteuthis pealeii* (MLs=29.9–31.8 cm), were found in wahoo stomachs in the SAB during fall, and the smallest cephalopods included several early juvenile benthic octopods (MLs=0.5–1.0 cm) recovered from the stomachs of yellowfin and albacore tunas landed in NE during late summer in multiple years. It is noteworthy that two beaks of the pelagic octopod, *Haliphron atlanticus* (LHLs=14.92

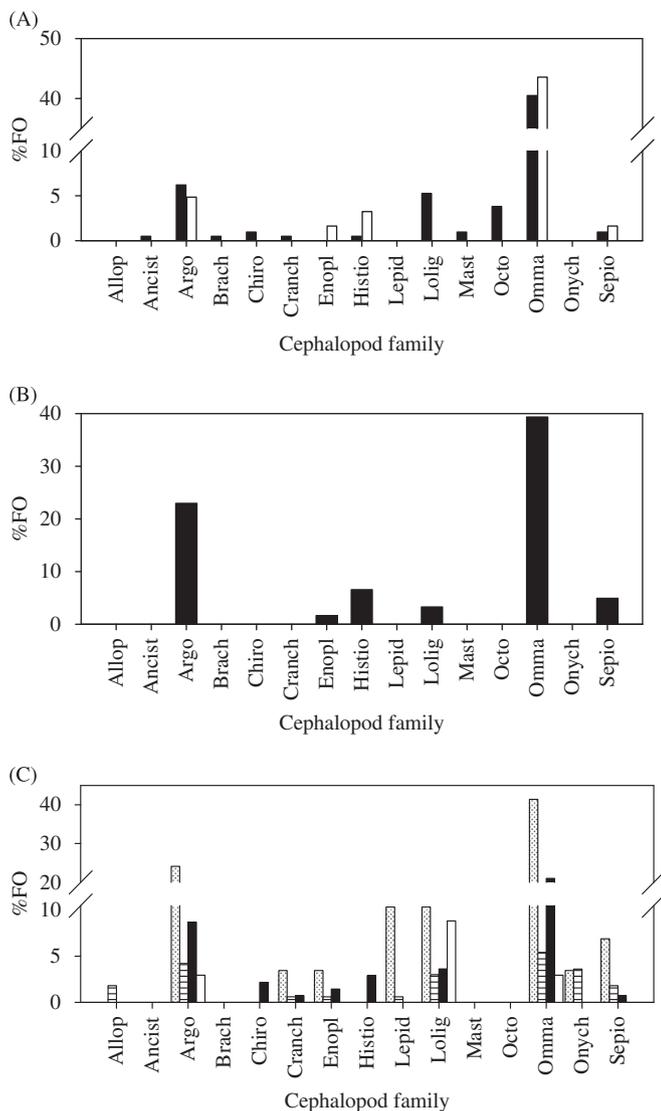


Fig. 1. Percent frequency of occurrence (%FO) of cephalopod families, Alloposidae (Alloposidae), Ancistrocheiridae (Ancist), Argonautidae (Argo), Brachioteuthidae (Brach), Chiroteuthidae (Chiro), Cranchiidae (Cranch), Enoploteuthidae (Enopl), Histio-teuthidae (Histio), Lepidoteuthidae (Lepid), Loliginidae (Lolig), Mastigoteuthidae (Mast), Octopodidae (Octo), Ommastrephidae (Omma), Onychoteuthidae (Onych), Sepiidae (Sepio), found across all predator stomachs sampled in the (A) New England, (B) Mid-Atlantic Bight, and (C) South Atlantic Bight regions during spring (horizontal stripes), summer (closed bars), fall (open bars), and winter (dotted). Note that sampling was not conducted during all seasons in each region. The number of predators sampled in each region is listed in Table 1.

and 13.18 mm) were recovered from two dolphinfish stomachs landed in the SAB in May 2011. *H. atlanticus* is known to reach large body sizes of up to 2 m total length (Nesis, 1987). To the best of our knowledge a published equation for reconstructing mantle length does not appear in the literature for *H. atlanticus*; however, beaks sizes and pigmentation suggest that large adults were consumed.

Prey size varied significantly among predator diets ($F=74.3$, $df=1473$, $p < 0.0001$) with the largest cephalopods on average consumed by deep diving predators including porbeagle (mean ML=16.5 cm) and thresher sharks (mean ML=14.9 cm), and the smallest cephalopods were consumed by blackfin (mean ML=5.2 cm), albacore (mean ML=6.1 cm), and yellowfin tunas (mean ML=8.0 cm) (Fig. 2).

Significant differences in *Argonauta* sp. body sizes were detected among regions ($H=13.4$, $df=2$, $p=0.0012$). The largest

individuals of *Argonauta* sp. were present in predator diets from the MAB (mean LHL=3.33 mm), the smallest were from NE waters (mean LHL=2.03 mm), and individuals from the SAB were intermediate (mean LHL=2.27 mm) (Fig. 3). Body sizes of *I. illecebrosus* also differed significantly among regions ($H=158.1$, $df=2$, $p < 0.0001$); larger individuals were found in the MAB (mean LRL=2.45 mm) compared to NE (mean LRL=2.13 mm) and the SAB (mean LRL=1.45 mm) (Fig. 4). Based on length-at-age estimates from Hendrickson (2004) it was assumed that *I. illecebrosus* < 3.5 cm ML were paralarvae, 3.5–6.5 cm ML were juveniles, and ≥ 6.5 cm were adults; we estimate that 72.5% of all *I. illecebrosus* consumed by predators were adults, 23.7% juveniles, and 3.8% paralarvae. Tunas foraging in the SAB consumed the majority (55%) of all paralarval and juvenile *I. illecebrosus* found across all predator diets and regions. Early juvenile *I. illecebrosus*, and benthic octopods were also found in the diets of yellowfin and albacore tunas in NE during multiple years, while juvenile longfin squid (*D. pealeii*) (< 5 cm ML) and early juveniles from the family Lepidoteuthidae (1.8–5.1 cm ML) were present in blackfin tuna diets in winter and spring in the SAB.

Regional comparisons could not be performed on other species due to small sample sizes, thus size distributions for *D. pealeii*, *Ornithoteuthis antillarum*, *Abralia* sp., and sepiolids were pooled across spatiotemporal scales and are presented in Fig. 5.

4. Discussion

4.1. Dietary results

Similar to previous studies in other regions, our findings emphasize the value of using predators as biological samplers to gain information on cephalopod distribution, abundance, diversity, and importance in seasonal food-webs (Cherel et al., 2004; Clarke, 2006; Peristeraki et al., 2005; Spitz et al., 2011). Global descriptions of the biogeography and trophic roles of cephalopods are relatively deficient compared to other marine taxa, and this is particularly true in the Northwest Atlantic. Prior evaluations in this region have rarely provided detailed descriptions of the cephalopod component of predator diets (e.g., Chase, 2002; Rudershausen et al., 2010), and nets are known to be ineffective in capturing all species and sizes of cephalopods present in the environment (Cherel et al., 2004; Clarke, 2006, 1980). Results of the present study are in agreement with mid-water and bottom-trawl survey findings that ommastrephid, enoploteuthid, and histio-teuthid squids are generally the most abundant cephalopod families occurring in epipelagic (≤ 200 m) and mesopelagic (200–1000 m) waters of the Northwest Atlantic (Vecchione, 2001; Vecchione and Galbraith, 2001; Vecchione and Pohl, 2002). Argonauts were the primary octopod, and second most important cephalopod overall in predator diets. However, argonauts are notably absent from trawl surveys in the region suggesting that predators are either selectively feeding on them or argonauts are able to avoid capture by traditional survey methods (Clarke, 2006; Vecchione, 2001; Vecchione and Galbraith, 2001; Vecchione and Pohl, 2002).

Argonauts were reported as primary prey to Risso's dolphin (*Grampus griseus*) in the western Mediterranean Sea (Blanco et al., 2006), and have also been found in the diets of a variety of tunas, billfish, dolphinfish, wahoo, and lancetfish (*Alepisaurus ferox*) in the Atlantic Ocean (Chase, 2002; Gibbs and Collette, 1959; Manooch and Mason, 1983), Pacific Ocean (Olson and Galvan-Magana, 2002; Shimose et al., 2010), West Indian Ocean (Potier et al., 2007), Mediterranean Sea (Peristeraki et al., 2005), Gulf of Mexico (Manooch and Hogarth, 1983), and off the eastern coast of Australia (Young et al., 2010). The frequent occurrence of

Table 4

Regional contribution of cephalopod prey to predator diets by percent mass (%M) in grams, number (%N), frequency of occurrence (%FO), and index of relative importance (%IRI) in waters of New England (NE), mid-Atlantic Bight (MAB), and the South Atlantic Bight (SAB). *N* indicates the number of fish sampled.

Predator species	New England					Mid-Atlantic Bight					South Atlantic Bight				
	<i>N</i>	% <i>M</i>	% <i>N</i>	% <i>FO</i>	% <i>IRI</i>	<i>N</i>	% <i>M</i>	% <i>N</i>	% <i>FO</i>	% <i>IRI</i>	<i>N</i>	% <i>M</i>	% <i>N</i>	% <i>FO</i>	% <i>IRI</i>
Coryphaenidae															
Dolphinfish	110	46.7	6.7	42.7	29.8	9	< 1.0	2.2	22.2	0.3	174	14.2	6.9	21.9	4.5
Scombridae															
Albacore tuna	23	61.3	19.6	78.3	46.6	–	–	–	–	–	–	–	–	–	–
Bigeye tuna	2	99.8	91.5	100.0	95.7	1	98.9	92.9	100.0	95.9	1	< 1.0	16.7	100.0	–
Blackfin tuna	–	–	–	–	–	–	–	–	–	–	91	13.3	32.8	52.9	31.3
Yellowfin tuna	80	49.5	12.3	76.3	33.7	14	24.5	18.3	85.7	19.3	14	2.4	35.9	76.9	33.3
Wahoo	11	< 1.0	28.9	27.3	9.5	4	29.0	15.0	75.0	46.1	86	1.3	30.8	16.3	5.5
Isiophoridae															
Roundscale spearfish	–	–	–	–	–	9	12.8	25.5	55.6	12.9	–	–	–	–	–
White marlin	–	–	–	–	–	20	21.1	53.5	72.2	33.5	–	–	–	–	–
Xiphiidae															
Swordfish	3	97.4	88.8	100.0	94.1	–	–	–	–	–	–	–	–	–	–
Elasmobranchii															
Porbeagle shark	3	81.3	57.6	66.7	63.6	–	–	–	–	–	–	–	–	–	–
Shortfin mako shark	29	< 1.0	14.5	24.1	2.7	–	–	–	–	–	1	100.0	100.0	100.0	100.0
Thresher shark	33	< 1.0	< 1.0	15.2	0.2	–	–	–	–	–	–	–	–	–	–

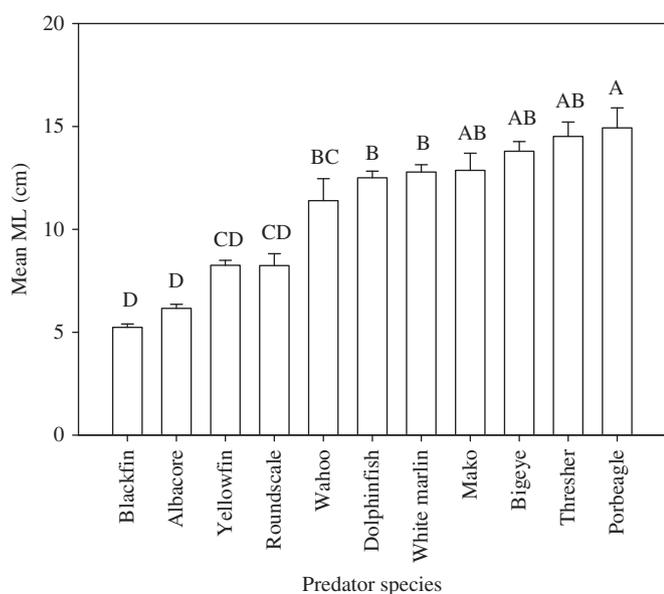


Fig. 2. Mean mantle lengths (cm) ± standard error of cephalopods found in predator diets. Data are representative of collections from pelagic waters along the US Atlantic coast from Massachusetts to South Carolina. Means with the same letter are not significantly different from each other (Tukey–Kramer test, $p < 0.05$).

argonauts in the diets of numerous pelagic predators demonstrates they are widely abundant and available prey in global epipelagic habitats.

Although *A. argo* is believed to be the more common of the two Argonaut species found in Northwest Atlantic waters (Finn, 2010), results are presented to the level of genus because it was not possible to differentiate between the beaks of *A. argo* and *A. hians*. Additionally, due to the extreme sexual dimorphism of argonauts (Wu, 1989), it is unclear whether observed differences in regional size distributions reflect disparities in life stages or the composition of males and females in the population. A better understanding of how patterns in beak pigmentation vary with sexual maturity is needed before this relationship can be used to explain population demographics of argonauts.

Ommastrephids are one of the most commonly reported squid prey in top predator diets from other ocean basins including the tropical Atlantic, Pacific, Indian, and Mediterranean Sea (Cherel et al.,

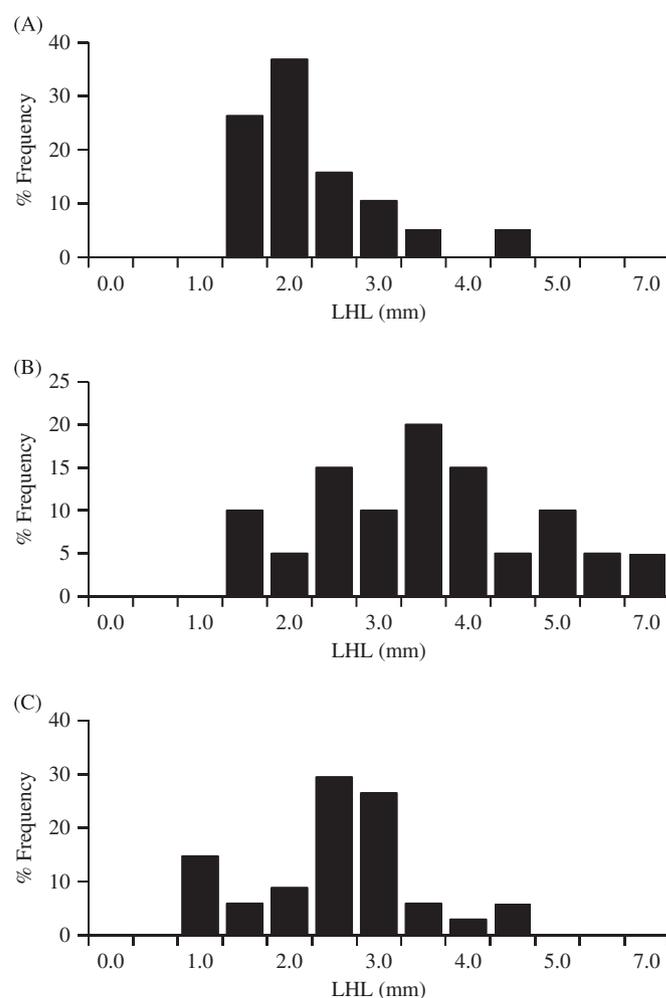


Fig. 3. Size frequency distributions of lower hood length (LHL) measurements in millimeters for *Argonauta* sp. recovered from the diets of predators caught in waters off of (A) New England, (B) the Mid-Atlantic Bight, and (C) the South Atlantic Bight. LHLs were grouped in 1 mm increments for display purposes.

2007; Olson and Galvan-Magana, 2002; Peristeraki et al., 2005; Potier et al., 2007; Young et al., 2010). Due to their commercial importance, ommastrephids are one of the few cephalopod taxa whose biology is

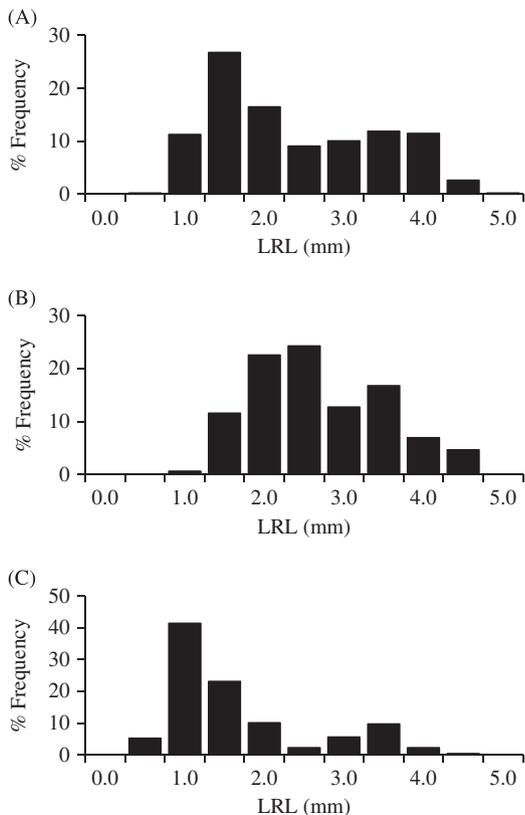


Fig. 4. Size frequency distributions of lower rostral length (LRL) measurements in millimeters for *Illex illecebrosus* recovered from the diets of predators caught in waters off of (A) New England, (B) the Mid-Atlantic Bight, and (C) the South Atlantic Bight. LRLs were grouped in 1 mm increments for display purposes.

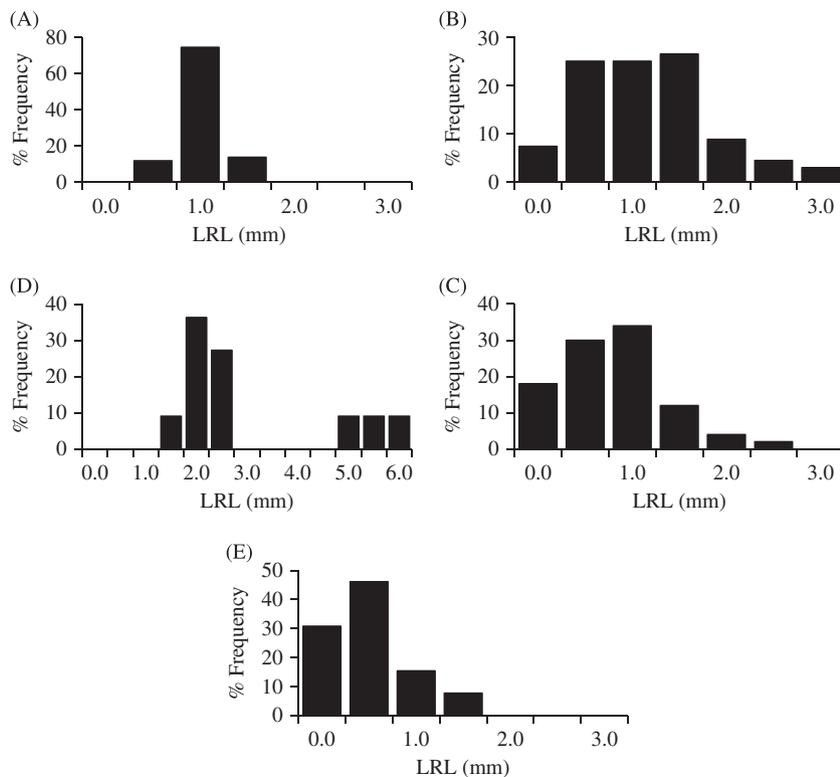


Fig. 5. Size frequency distributions of lower rostral length (LRL) measurements in millimeters for (A) *Abralia* sp., (B) *Doryteuthis pealeii*, (C) *Ornithoteuthis antillarum*, (D) *Histioteuthis reversa* (LRLs < 3.0 mm) and *H. bonnellii* (LRLs ≥ 5.0 mm), and (E) *Sepiolidae* uncl. recovered from predator diets collected across all regions.

fairly well described; however, key aspects of the life history and population structure of *I. illecebrosus* remain unresolved including spawning location, and offshore population structure (Hendrickson, 2004; Rowell et al., 1984). Previous studies have documented *I. illecebrosus* as primary cephalopod prey to swordfish (Stillwell and Kohler, 1985), blue sharks (*Prionace glauca*) (Kohler, 1987), long-finned pilot whales (*Globicephala melas*) (Gannon et al., 1997), and a range of other teuthophagous predators throughout the Northwest Atlantic Ocean (Dawe and Brodziak, 1998). Our findings reinforce the importance of ommastrephids, particularly *I. illecebrosus* as a vital prey species shared by multiple commercially and ecologically important fishes in open ocean food-webs.

Comparatively less is known about the smaller and unexploited Ommastrephid species, *O. antillarum*. *O. antillarum* is common in warm slope waters of the Northwest Atlantic, although it does not form schools as large as *I. illecebrosus* (Vecchione and Galbraith, 2001). This species is reported as recurrent prey in tuna and billfish diets off of South America (dos Santos and Haimovici, 2002). Because of its similar characteristics to *I. illecebrosus* this species may often be misidentified and under-reported as prey in regional studies.

A. veranyi, a small mesopelagic squid, was an occasional prey across predators and regions; however, the occurrence of 53 individuals in a single yellowfin tuna stomach during fall of 2007, and additional incidences during late summer and early fall during other years indicates this species may be aggregating in large numbers, most likely to spawn, in waters off of New England. Heightened predation on cephalopod spawning grounds has been documented in other parts of the world (Rosa and Seibel, 2010; Smale et al., 2001). Consequently, *A. veranyi* may be an important seasonal prey resource to opportunistic predators.

H. reversa and *H. bonnellii* are relatively common in slope waters of the Northwest Atlantic (Vecchione, 2001; Vecchione and Pohl, 2002), and often dominate the diets of deep-diving

odontocetes (Clarke, 1996; Santos et al., 2006; Spitz et al., 2011). Many fishes examined in this study are thought to feed primarily in epipelagic waters (Young et al., 2010), and likely encounter histioteuthids at night when squids migrate vertically from mesopelagic waters to the surface in pursuit of prey (Voss et al., 1998). Alternatively, depending on water temperatures and time of day fish may dive into deeper waters to exploit mesopelagic prey resources (Pusineri et al., 2008; Sepulveda et al., 2011; Weng et al., 2009). The relatively small numbers of histioteuthids in fish diets compared to marine mammal diets such as pygmy sperm (Kogia breviceps), and long-finned pilot whales (Gannon et al., 1997; Santos et al., 2006; Spitz et al., 2011) suggests foraging depth is a key dimension segregating the ecological niches of large pelagic fishes and marine mammals in outer shelf and slope habitats.

4.2. Spatiotemporal size distributions

In addition to quantifying the role cephalopods play as prey in the Northwest Atlantic, information gained from teuthophagous predators provides insight into the life history and spatiotemporal distributions of poorly known cephalopods. In the present study, small sample sizes limited evaluations of spatial distributions to two species groups, *Illex* sp. and *Argonauta* sp. Our results showed the largest argonauts were present in the MAB and suggest the presence of both mature males and females (ML in females reaches 12 cm, whereas males only attain 1.5–2.0 cm, Jereb and Roper, 2005). In addition, multiple gravid females were found in the diets of dolphinfish landed off the coast of North Carolina during the month of May. Although argonauts are considered solitary animals, female *A. nouryi* are known to form chains in the eastern tropical Pacific and off of South Africa, presumably to increase their chances of encountering males and reproducing (Rosa and Seibel, 2010). Similar to observations of *A. nouryi* by Rosa and Seibel (2010), *A. hians* in the Andaman Sea (Sukhsangchan et al., 2009), and *A. argo* in the Mediterranean Sea (Salman, 2004), our results suggest aggregative spawning behaviors also occur in the Northwest Atlantic. Relatively small individuals, possibly paralarval or juvenile argonauts were found in New England waters. Because paralarval distributions of this species are collected over a narrow range of temperatures (Vecchione et al., 2001), our collections suggest a juvenile migration into northern waters in the summer with a return migration to the MAB and SAB (where they were found in winter collections) in the fall and winter.

A similar pattern was found in the regional size distribution for *I. illecebrosus*, except that the smallest individuals were found in the SAB primarily in the winter and spring. *I. illecebrosus* is a pelagic spawner with peak spawning in the winter and spring off the coast of Florida where sea temperatures are warm enough for embryonic development (O'Dor, 1983; Vecchione et al., 2001). A second, smaller spawning effort occurs during summer in the MAB (Coelho et al., 1994). Hatchlings are carried north by the Gulf Stream. Consequently, it was expected that mean sizes of *I. illecebrosus* would increase with latitude; instead the largest sizes were found in the MAB in the summer, perhaps due to the presence of spawning adults. *I. illecebrosus* is generally distributed from the shelf break out to more oceanic habitats but migrate over the continental shelf in the summer (Black et al., 1987; Mesnil, 1977). There is also evidence from tagging studies that males mature and migrate earlier than females (O'Dor, 1983). Regional size differences may thus reflect seasonal and/or sex- and size-specific differential migration patterns. Alternatively, distributions of cephalopod body sizes may be influenced by differences in the species and sizes of predators sampled

seasonally in each of the three regions and their respective feeding preferences.

Little can be concluded from the size distributions of the remaining species other than in most cases the size ranges collected encompass paralarval, juvenile, and adult life stages. For example, male and female *O. antillarum* in the eastern Atlantic mature at 8.0–9.0 cm ML with no significant size differences between sexes or across latitudes and seasons (Arkhipkin et al., 1998). This species undergoes extensive diel vertical migrations from 600–800 m during the day and into surface waters at night (Jereb and Roper, 2010). Future studies that are able to collect data on the time and exact location of predator capture may provide additional information on the migratory behavior of *O. antillarum*.

Despite their trophic importance to teleosts, elasmobranchs, and marine mammals feeding in continental shelf waters of the Northwest Atlantic (Staudinger and Juanes, 2010a), relatively few *D. pealeii* were collected in this study. This pattern may be due to the more coastal and inshore distribution of *D. pealeii* relative to *I. illecebrosus* (Black et al., 1987), and reflects the more slope-based foraging habits of the large pelagic predators sampled here.

4.3. Predation on paralarval and juvenile life stages

Although juvenile cephalopods are considered important components of oceanic food-webs, there is a general lack of information on predation on early life stages (Bello and Pipitone, 2002). This is due in part because small cephalopods are digested more rapidly than larger ones, and the small and fragile beaks from young individuals are easily degraded and destroyed in predator stomachs (Santos et al., 2001). In addition, beaks from young cephalopods are difficult to identify because morphological characteristics known in adults may not have fully formed. Beaks were the primary structures used in this study to identify species, and classification of relatively common species (e.g., *I. illecebrosus*) required comparisons with reference collections at the National Museum of Natural History (NMNH) before identifications could be made with confidence.

Similar to studies conducted in the Adriatic Sea (Bello, 1999), the Bay of Biscay (Pusineri et al., 2005), French Polynesia (Ménard et al., 2006), the Indian Ocean (Roger, 1994), and the Caribbean Sea (Headley et al., 2009), our results show that most tunas consumed very small squids and octopods. Bigeye tuna was the exception. Significantly larger cephalopods were found in the bigeye diet compared to yellowfin, blackfin, and albacore tunas. Comparisons between bigeye and yellowfin tunas in the Pacific Ocean have also shown that bigeye select for larger prey sizes than yellowfin and albacore tunas (Ménard et al., 2006; Young et al., 2010). The thermoregulatory abilities of bigeye tuna allow them to penetrate the thermocline and access deep, mesopelagic waters where a greater range of prey species and sizes reside; consequently, this gives bigeye a competitive advantage over yellowfin and albacore tunas which are typically restricted to the epipelagic zone (Brill, 1994; Ménard et al., 2006; Pusineri et al., 2008). Very few bigeye tuna were sampled as part of this study thus although individuals included in our analyses were found to consume large squids, additional samples are needed to make definitive conclusions about the overall diet and feeding patterns of bigeye tuna in this region.

Inter-annual and seasonal fluctuations in prey availability are primary factors influencing the migration patterns and distributions of large pelagic predators in regional ecosystems (Kitchell et al., 1978; Olson and Boggs, 1986). The large quantities of paralarval and juvenile *I. illecebrosus*, *D. pealeii*, and lepidoteuthids found in yellowfin and blackfin tuna diets during spring indicates these are seasonally important prey resources in the South

Atlantic Bight. In addition, tunas and other apex predators play a major role in structuring marine communities through consumption (Olson and Boggs, 1986). Consequently, tuna predation can potentially have a significant impact on the recruitment and survival of the commercially important stocks of *I. illecebrosus* and *D. pealeii*.

I. illecebrosus spawn in waters of the South Atlantic during winter as well as in the Mid-Atlantic Bight during summer and early fall, although this has never been observed in the wild (Hendrickson, 2004; Rowell et al., 1984; Vecchione, 2001). Based on the prevalence of paralarval and juvenile *I. illecebrosus* in predator diets landed off of North Carolina during February and March, our results provide further evidence of a spawning ground in this region, likely during December and January. The occurrence of early juvenile lepidoteuthids in blackfin tuna diets during February may also reflect a winter spawning site, and essential habitat for early life stages of either *Lepidoteuthis grimaldii* or *Taningia danae* in the South Atlantic. Lepidoteuthids are rarely captured in surveys and virtually unknown in regional waters (Jereb and Roper, 2010); therefore, reports of their occurrence in predator diets may provide critical information on their biology.

4.4. Caveats and conclusions

Fisheries-dependent sampling (e.g., long-line and hook and line fisheries) has been an important source of ecological data for many of the predator species included in this study (Chase, 2002; Manooch and Hogarth, 1983; Manooch and Mason, 1983; Rudershausen et al., 2010); however, because data collected from recreational and commercial fisheries are biased in the sizes of fish they catch, as well as the time of day and areas (e.g., depth, distance to shore) where fishing occurs, results may only represent a subset of predator–prey interactions in the greater community. In the present study, access to predators was limited by their seasonal occurrence in each region, and subject to recreational angler behavior. Most recreational anglers fish in waters that can be reached by day-trips from the shore, hence descriptions of cephalopod fauna presented in this study likely reflect seasonal assemblages in epipelagic waters of the shelf-slope edge and Gulf Stream. However, all of the predators sampled in this study are considered highly migratory, and the distances traveled between their last meal and capture is unknown (Markaida and Hochberg, 2005).

Although collections were conducted nearly year-round in the South Atlantic Bight, sampling effort was limited to late summer and early fall in New England and the Mid-Atlantic Bight. In addition, sample sizes from the Mid-Atlantic Bight, and predators such as bigeye tuna, swordfish, and porbeagle sharks were very small and should be viewed as preliminary. Other factors including regurgitation, the time of day when predators were captured, digestion times and accumulation rates of beaks in predator stomachs, and the types of gear used to harvest predators also likely influenced our results. Despite these limitations, using predators as biological samplers revealed unique and fundamental information on the cephalopod community and predator–prey interactions in the Northwest Atlantic region. Additional studies that utilize other sampling methodologies (e.g., gear types), and survey over greater spatial and temporal scales will be useful to gain a more comprehensive view of community relationships in this region. For example, stable isotope analyses of predator and cephalopod tissues would complement stomach content analysis by providing assessments of trophic position, habitat use, as well as seasonal and ontogenetic shifts in community structure (Chippis and Garvey, 2007; Fry, 2006).

Using predators as biological samplers is an alternative approach to traditional fisheries surveys, and has provided insight

into the availability and distribution of cephalopods in a range of marine ecosystems (Cherel et al., 2004, 2007; Clarke, 2006; Peristeraki et al., 2005; Spitz et al., 2011). Although many of the predators sampled in this study are thought to feed opportunistically, underlying factors (e.g., behavior, morphology) that influence predator selectivity may be influencing the sizes and species of cephalopods found in their diets (Link, 2004; Staudinger and Juanes, 2010b; Werner, 1974). Comparisons of cephalopods occurring in predator diets and surveys will help identify species that may be selectively captured or avoided by predators and nets (Clarke, 2006; Staudinger and Juanes, 2010a). Because of the paucity of survey data on cephalopod diversity patterns (Tittensor et al., 2010), information from predators should be considered by future studies to supplement records on species that are not targeted by fisheries or not regularly caught by survey gear (e.g., Argonautidae, Lepidoteuthidae). Monitoring the occurrence and relative abundance of cephalopods as well as other prey in predator diets may also assist in recognizing and tracking community changes brought about by climate change, exploitation, and other anthropogenic stressors. Sampling multiple predators that forage across a range of depths could provide insight into how cephalopods and other fauna are shifting their latitudinal and depth ranges in response to environmental changes (Clarke, 2006). For example, diet comparisons of deep-diving predators (e.g., bigeye tuna, swordfish and toothed whales) with predators that are generally restricted to surface waters (e.g., dolphinfish, wahoo, and yellowfin tuna) would provide coverage from epipelagic to mesopelagic and bathypelagic habitats. In addition, opportunistic predators that are widely available such as yellowfin tuna may serve as indicators of latitudinal shifts in prey composition and importance.

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