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Trophic ecology of the deep-sea cephalopod assemblage near Bear Seamount in the Northwest Atlantic Ocean

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ABSTRACT: Cephalopods compose a vital component of marine food webs worldwide, yet their trophic roles remain largely unresolved. This study used stable carbon and nitrogen isotopes to describe the trophic structure, ontogeny, and isotopic niche overlap of cephalopod groups from pelagic and near-bottom habitats around Bear Seamount in the Northwest Atlantic Ocean. Beaks from 225 specimens (13 families; 27 species), primarily from juvenile and sub-adult life stages, were collected during a deep-sea biodiversity cruise conducted in 2012. Differences in mean $\delta^{15}N$ and $\delta^{13}C$ values were detected among some families and across species within the families Ommastrephidae, Histioteuthidae, Mastigoteuthidae, and the superfamily Argonautoidea. Trophic positions ranged from 2.7 to 4.5 across assemblage members, with top positions held by *Illex illecebrosus*, *Histioteuthis reversa*, *Octopoteuthis sicula*, *Taonius pavo*, and *Haliphron atlanticus*. Cephalopod families exhibiting the broadest and most diverse isotopic niche widths overall included Ommastrephidae, Cranchiidae, and Octopoteuthidae. Families with the narrowest isotopic niches included Onychoteuthidae and the monospecific Joubiniteuthidae, and Vampyroteuthidae. Trophic position increased significantly with body size (mantle length) across all individuals sampled, and ontogenetic shifts in $\delta^{15}N$ values were detected in 7 species. The continuous gradient and broad range of isotope values across families, species, and body sizes suggest an unstructured assemblage comprised of generalist and specialist foragers distributed throughout a vertical depth range of pelagic (depleted $\delta^{13}C$ values) to near-bottom bathy/benthopelagic (enriched $\delta^{13}C$ values) habitats. The results provide some of the first quantitative trophic metrics for many poorly studied species and advance our understanding of the diversity of cephalopod ecological roles in marine ecosystems.

KEY WORDS: Cephalopods · Deep-sea · Mesopelagic · Bathy/benthopelagic · Seamount · Stable isotope analysis · Community structure · Trophic position · Ontogenetic shifts

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1. INTRODUCTION

Cephalopods compose a vital component of marine food webs worldwide. They are generally known as primary forage for predators of ecological and conservation importance including teleosts, elasmobranchs, marine mammals, and seabirds (Smale 1996, Dawe & Brodziak 1998, Staudinger & Juanes 2010, Staudinger et al. 2013, Teffer et al. 2015, Xavier et al. 2018). Cephalopods are also important consumers of secondary producers (e.g. zooplankton), fishes, other cephalopods, and gelatinous animals (e.g. medusa, siphonophores, and ctenophores) (Hunsicker & Essington 2006, 2008, Martínez-Baena et al. 2016, Rosas-Luis et al. 2016, Choy et al. 2017, Hoving & Haddock 2017). Because of their generalist foraging habits, fast growth rates and high energetic demands, cephalopods serve as a critical intermediate link and conduit between lower and upper trophic levels in marine food webs (Boyle & Rodhouse 2005, Hunsicker & Essington 2008). Nonetheless, the specific functional roles of many species as well as the trophic structure of cephalopod assemblages, especially in the deep sea, remain largely unknown (Cherel et al. 2009a,b, Coll et al. 2013). Mesopelagic and bathy/benthopelagic species occupying deep-sea environments off the continental slope and in the open ocean live at depths that are not well sampled with any regularity. Some species avoid survey gear through strong swimming capabilities, while more gelatinous species are prone to damage during sampling and therefore difficult to collect. Much of what we do know about the trophic roles of offshore and deep-sea cephalopods has been determined from digested remains found in the stomachs of their predators, including marine mammals, seabirds, and fishes (Clarke 1996, Croxall & Prince 1996, Klages 1996, Smale 1996, Clarke 2006, Cherel et al. 2007). Using predators as biological samplers has been a crucial method to obtain information on rare or elusive species but, to date, has been limited to understanding cephalopod's trophic role as prey (Cherel & Hobson 2005, Young et al. 2010, Logan & Lutcavage 2013, Staudinger et al. 2013).

Because cephalopods take small bites out of their prey and have high digestion rates, using traditional stomach content analysis to determine what they are eating is subject to inherent biases (e.g. towards prey where hard parts were consumed) and may not fully capture their complete diets (Martínez-Baena et al. 2016, Rosas-Luis et al. 2016). In comparison, molecular techniques (e.g. DNA barcoding) and biochemical tracers such as fatty acids and stable isotopes have led to recent advances in resolving cephalopod feeding habits and trophic roles (Ruiz-Cooley et al. 2004, Cherel & Hobson 2005, Parry 2006, Cherel et al. 2009a,b, Guerra et al. 2010, Navarro et al. 2013). Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are useful for inferring foraging ecology and trophic relationships, with consumer tissues becoming more enriched in δ^{15}N and corresponding to increasing trophic level as the lighter isotope δ^{14}N is excreted (Post 2002, Fry 2006). δ^{13}C values provide information about sources of primary production at the base of different food webs in which animals are feeding throughout their life history (Cherel & Hobson 2005). In marine environments, relatively negative δ^{13}C values indicate offshore or pelagic habitats, while relatively positive δ^{13}C values indicate inshore or near bottom (demersal and benthic) environments (Graham et al. 2010, Oczkowski et al. 2016). Various tissue types reflect different isotopic time-frames ranging from weeks to months based on organ-specific fractionation rates and turnover times (Logan et al. 2008). In cephalopods and other soft-bodied animals, measuring isotope values from hard tissues such as beaks, statoliths, and eye lenses offers unique opportunities to elucidate trophic roles and ontogenetic shifts in comparison with soft tissues (e.g. mantle muscle). Hard tissues, beaks in particular, may be derived from specimens collected during new and historical studies that represent both direct collections (e.g. from biodiversity cruises) or indirectly acquired from investigations of their predators (Staudinger et al. 2014, Seco et al. 2016).

Studies utilizing stable isotopes to investigate the trophic ecology of cephalopods both in terms of their foraging habits and their roles as prey are increasing in number and scope (Coll et al. 2013, Navarro et al. 2013), with notable advances from studies of the Southern (e.g. Cherel & Hobson 2005, Guerreiro et al. 2015, Rosas-Luis et al. 2016), Pacific (e.g. Madigan et al. 2012, Choy et al. 2015), Arctic (Golikov et al. 2018), and Northeast Atlantic Oceans (e.g. Cherel & Hobson 2005, Cherel et al. 2009b, Merten et al. 2017). While some evidence exists for a structured cephalopod trophic assembly in polar regions (e.g. Cherel & Hobson 2005, Guerreiro et al. 2015, Golikov et al. 2018), midwater cephalopods appear to form unstructured assemblages comprised of generalist foragers (e.g. Cherel et al. 2009b, Madigan et al. 2012, Choy et al. 2015, Rosas-Luis et al. 2016, Merten et al. 2017). However, fewer studies exist for cephalopods in the Northwest Atlantic Ocean. A recent study by Shea et al. (2017) reported that 77 cephalopod species occur in pelagic and benthic waters surrounding Bear Seamount. This extinct undersea volcano located south of Georges Bank is one of >30 seamounts that comprise the New England Seamount chain and is central to the newly designated New England Canyons and Seamounts Marine National Monument. Pelagic and bathyal habitats above and surrounding Bear Seamount are influenced by the Gulf Stream and the deep Western Boundary undercurrents, bringing a mixture of warm and cold water masses, respectively, and stimulating upwelling and mixing (Moore et al. 2003). The influence of such diverse oceanographic processes, along with complex topography and heterogeneous habitats, fosters high biodiversity (Clark et al. 2012) and makes this an ideal system to explore a broad range of cephalopod taxa. Here, we use stable isotopes of carbon and nitrogen to quantify trophic aspects of assemblage structure and ontogeny as well as individual trophic roles of an array of cephalopod species and families. The diversity of the Bear Seamount assemblage has been shown to be representative of the broader Northwest Atlantic (Vecchione & Pohle 2002, Vecchione et al. 2010, Shea et al. 2017); therefore, this study offers novel insights into regional deep-sea ecosystem structure and function.

2. MATERIALS & METHODS

2.1. Sample collection

A deep-sea biodiversity survey of Bear Seamount, between 39° 45′ and 40° 00′ N and between 066° 55′ and 067° 40′ W in the Northwest Atlantic Ocean (Fig. 1), was conducted between 30 August and 7 September 2012 by the National Marine Fisheries Service aboard the NOAA ship 'Pisces'. A total of 27 midwater and 2 bottom tows were conducted. Midwater sampling used a Superior double-warp trawl rigged with deep-water floats and White Nets midwater doors (Table A1 in the Appendix). These open tows averaged 51 min at target depths, and net monitoring indicated sampled depths ranging from 602 to 1921 m. Additionally, 2 bottom trawls using a 4-seam double-warp trawl rigged with deep-water floats and rock-hopper sweep with Perfect Doors were conducted for ~90 min across the flat top of the seamount at maximum depths of 1297 m. Fishes, cephalopods, other invertebrates, and vegetation were removed from the net mesh using forceps to ensure the majority of individuals remained intact and in good condition. All specimens were sorted by major taxonomic group, counted, and measured to the nearest millimeter (mm).

In total, 1150 mesopelagic and bathy/benthopelagic cephalopods representing ~62 species (confirmation at the species level was not possible for 15 specimens) were collected. Intact cephalopods were identified to the highest taxonomic resolution possible

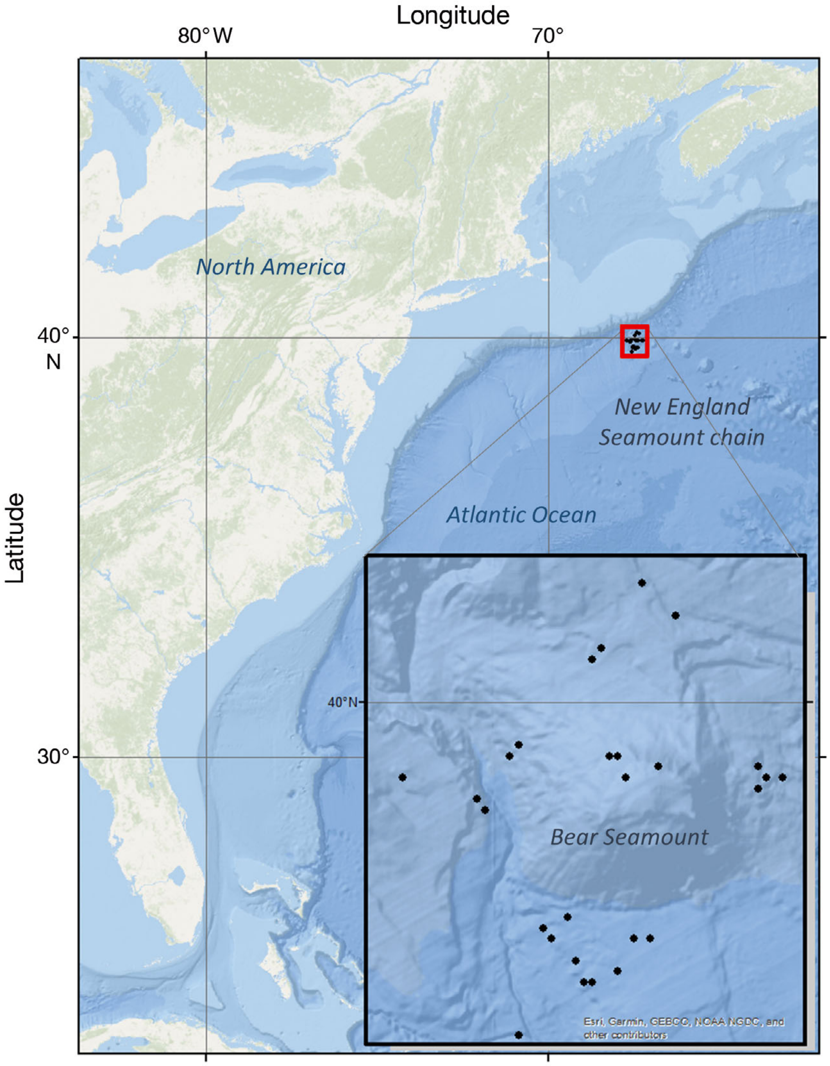

Fig. 1. The Northwest Atlantic region, the New England Seamount chain, and Bear Seamount, which is highlighted in the red box. Detailed station locations are shown in the inset map. Station locations represent tow start locations, and additional information on all midwater tows can be found in Table A1 in the Appendix

and measured for mantle length (ML). The buccal masses of 216 squids and octopods representing 26 species in 13 families were removed, frozen, and transported to the National Museum of Natural History in Washington, DC where they were later prepared and processed for stable isotope analyses.

Nine specimens of *Argonauta* sp. were also included in our analyses so their trophic ecology could be assessed relative to other co-occurring cephalopod species. Specimens of *Argonauta* sp. were recovered from the stomachs of white marlin *Tetrapturus albidus* and roundscale spearfish *T. georgii* caught in nearby waters of the continental slope just to the south and west of Bear Seamount. Beaks that exhibited little to no signs of erosion from digestion or were from partially intact individuals (i.e. tissue and external egg-cases were partially present) were used in an effort to evaluate specimens that were consumed recently and had the highest likelihood of being from nearby waters.

Lower and upper beaks from all cephalopods were extracted from the buccal masses, cleaned of remaining tissue, and photographed for reference, and the lower rostral length (LRL) or lower hood length (LHL) was measured. Maturity stage was classified as either juvenile, sub-adult, or adult based on the level of darkening and transparency present in the lateral walls and wings (Cherel et al. 2009a). Juveniles were designated when the lateral walls and wings of the beak were almost completely transparent; subadults when the lateral walls and/or wings of the beak were darkening but edges showed some transparency; adults were defined when beaks were completely darkened with no visible transparent portions. The majority of beaks were classified as juveniles or subadults, and only 3 individuals (*Chiroteuthis mega*, *Vampyroteuthis infernalis*, and *Bolitaena pygmaea*) were designated as adults.

2.2. Stable isotope analysis (SIA)

The formation and chemical composition of cephalopod beak tissue varies with growth and development. Beaks darken with growth, and the level of transparency or darkness serves as an indicator of maturity (Cherel et al. 2009a). Younger beaks contain a higher proportion of chitin, while the darkened portions of the beak are made up of a mixture of chitin and proteinaceous material (Cherel et al. 2009a). Relatively high carbon content in transparent portions of beak tissue often requires increased dilution for the mass spectrometer to produce adequate peaks for isotopic analysis. To determine the minimum amount of tissue needed to obtain isotopic results as well as to establish the degree of bias imposed by portions of the beak containing high chitin, a series of pilot samples was evaluated from the smallest sizes and earliest maturity stages of 5 species: *Leachia atlantica, Pyroteuthis margaritifera, Ornithoteuthis antillarum*, *Octopoteuthis sicula*, and *Magnoteuthis magna.* High C:N ratios (>4.0) were measured in transparent portions of beaks indicating chitin bias. For all subsequent analyses, lower beaks were processed by the systematic removal of transparent portions. This effectively eliminated chitin bias from the remaining samples, with 96% of individuals having C:N ratios ≤ 4.0 (species mean C:N range: 3.30 to 3.71). Values reported in this study therefore represent the integrated life history of each individual through approximately the sub-adult life phase.

All beak samples were rinsed with deionized water, placed into a drying oven at 65°C for 24 to 48 h, and homogenized using a mortar and pestle. Aliquots of homogenized beaks (<1.0 mg) were measured into tin cups and analyzed for $\delta^{15}N$, $\delta^{13}C$, wt %N, wt %C, and C:N ratios. Samples were loaded into a Costech Zero-Blank autosampler and combusted in a Costech 4010 Elemental Analyzer coupled to a Thermo Delta V Advantage continuous flow mass spectrometer at the Smithsonian Museum Conservation Institute. Isotope values were corrected to international reference materials using a 2-point linear correction on calibrated house standards: acetanilide and urea-UIN3 (Schimmelmann et al. 2009). Weight percent and C:N ratios were calculated based on known abundances in a homogenous acetanilide standard.

Stable isotope abundances are expressed in δ notation in per mille units (‰), according to Eq. (1):

$$\delta X = \left[\left(\frac{R_{\text{Sample}}}{R_{\text{standard}}}\right) - 1\right] \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, and R_{Sample} is the corresponding ratio ^{13}C:^{12}C or ^{15}N:^{14}N. The R_{standard} values were based on the Vienna PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N_2 for ^{15}N. Reproducibility based on replicate analyses of standards was <0.2‰ (1σ) for $\delta^{15}N$ and $\delta^{13}C$; all data presented here have an associated error of ±0.2‰ (1σ). Error associated with wt %N and wt %C is ±0.5% (1σ).

Because beak tissues are depleted in ^{15}N compared to soft tissues, raw values were adjusted by adding 3.5‰ following Cherel et al. (2009a,b). This correction factor was also applied so that cephalopod trophic positions could be related to results reported in regional studies of co-occurring competitors and predators (e.g. pelagic fishes and marine mammals).

2.3. Community structure and ontogenetic shifts

Differences in $\delta^{13}C$ and $\delta^{15}N$ values among and within major cephalopod families were tested using either a 1-way ANOVA or Kruskal-Wallis non-parametric analysis depending on whether assumptions of normality were met by each group of data. Pairwise multiple comparisons were made by applying the Tukey-Kramer or the Dunn's method for parametric and non-parametric tests, respectively. Linear regression was used to evaluate how trophic level (estimated from $\delta^{15}N$ values) and foraging habitat ($\delta^{13}C$) changed with increasing body size (ML) across the Bear Seamount cephalopod assemblage for all specimens with paired length and isotopic data, as well as for subsets of species with adequate sample sizes.

Trophic position was estimated for each species using $\delta^{15}N$ values of beak tissues following:

$$TP = \lambda + \frac{\delta^{15}N_{\text{Secondary consumer}} - \delta^{15}N_{\text{Base}}}{\Delta n} \qquad (2)$$

Stomatopod larvae, a common omnivorous zooplankton (Kline 2002) collected in the vicinity of Bear Seamount (N = 3), were chosen as a lower-trophic-level-organism representing Base for species distributed throughout midwater habitats and assigned a λ (TP) value of 2.5. A second baseline organism, *Munida valida*, was chosen to represent near-bottom benthopelagic habitats. This species was found to have a λ (TP) value of 2.7 in submarine canyons of a nearby deep-sea community (Demopoulos et al. 2017). For all calculations, Δn was assumed to be 3.4‰ on average and was the best trophic enrichment factor (TEF) available for deep-sea marine food web studies (Fry 1988, Post 2002).

2.4. Isotopic niche width and overlap

Bayesian ellipses were used to calculate and evaluate differences in isotopic niche width among cephalopod families (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Using this approach, isotopic niche width is measured as the standard ellipse area (SEA) in $\delta^{13}C$ and $\delta^{15}N$ space and is equivalent to standard deviation (SD) in univariate analyses. Standard ellipses were corrected for small sample sizes (SEAc) to compare the degree of isotopic niche overlap among major cephalopod families, where SEAc contains ~40% of the isotopic data and represents the mean core area of each group's isotopic niche. 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. 2011). Measures of niche diversity should be interpreted with some caution due to small and unequal sample sizes. Trophic similarity was assessed by calculating overlap between all pairwise combinations of family groups using size-corrected ellipses and then dividing the area (‰^{2}) of overlap by the combined areas (‰^{2}) of each pair of ellipses (Jackson et al. 2011). Two families, Bolitaenidae and Pyroteuthidae, were excluded from these analyses because they did not have adequate paired $\delta^{13}C$ and $\delta^{15}N$ values. All metrics were calculated using R (R Development Core Team 2016) v.3.5.3 and the statistical package SIAR and SIBER (Parnell et al. 2010).

3. RESULTS

3.1. Structure of the cephalopod assemblage at Bear Seamount

Overall, corrected values in cephalopod beaks ranged from +4.8 to +14.2‰ for $\delta^{15}N$ and −21.16 to −16.82‰ for $\delta^{13}C$ (Table 1, Fig. 2). Significant differences in mean $\delta^{15}N$ (H = 120.48, df = 12, $p < 0.001$) and $\delta^{13}C$ (H = 99.91, df = 12, $p < 0.001$) values were detected among all families (Table 2). Pairwise multiple comparisons (Dunn's) test showed the 13 families included in this analysis generally grouped into 1 of 3 tiers of $\delta^{15}N$ and $\delta^{13}C$ values (Table 2). Species with the most enriched $\delta^{15}N$ and $\delta^{13}C$ values included representatives from the families Mastigoteuthidae, Joubiniteuthidae, and Vampyroteuthidae, while squids from the families Onychoteuthidae, Ommastrephidae, and Enoploteuthidae exhibited the most depleted $\delta^{15}N$ and $\delta^{13}C$ values. The remaining families generally were intermediate to these high (enriched) and low (depleted) tiers (Table 2, Fig. 3A).

Trophic position increased with mantle length (N = 172) at a moderate but significant rate across all individuals sampled (R^2 = 0.19, F = 39.5, $p < 0.001$) and showed a stronger trend (Fig. 4A) than was found among species-specific values of trophic position and mantle length (R^2 = 0.13, F = 3.6, p = 0.07). High variability in trophic level was evident across all families and species (Fig. 5). Only a few individuals from the

Table 1. Summary of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values ± SD measured in cephalopod beaks. All measured isotopic values are reported. A correction factor of 3.5‰ was applied to raw $\delta^{15}N$ values following Cherel et al. (2009a,b). N indicates sample sizes; when 2 values are separated by a comma, the first number indicates sample size for $\delta^{13}C$ (‰), and the second indicates sample size for $\delta^{15}N$ (‰). Length indicates mantle lengths (mm) ± SD. Trophic position (TP) was estimated using the approach from Post (2002). *indicates species where TP was estimated using a bottom / benthopelagic baseline

Species	N	Mantle length (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	TP
Oegopsida						
Cranchiidae						
Leachia atlantica	7,1	61.1 ± 10.5	−17.9 ± 0.4	8.5 ± 0	3.46	3.52
Megalocranchia sp.	9	98.8 ± 60.0	−18.3 ± 1.2	9.7 ± 3.1	3.52	3.90
Taonius pavo	22,21	180.0 ± 50.6	−18.1 ± 0.6	10.5 ± 1.1	3.53	4.14
Chiroteuthidae						
_Chiroteuthis mega_*	9	81.4 ± 25.2	−18.2 ± 0.4	11.1 ± 1.4	3.49	3.10
_Chiroteuthis spoeli_*	4	92.3 ± 12.7	−18.0 ± 0.2	10.2 ± 1.2	3.52	2.84
_Chiroteuthis veranyi_*	3	49.5 ± 7.8	−17.7 ± 0.6	11.8 ± 1.8	3.63	3.31
Enoploteuthidae						
Abraliopsis morisii	12,13	27.7 ± 8.0	−18.3 ± 0.4	7.9 ± 1.0	3.30	3.37
Histioteuthidae						
_Histioteuthis bonnellii_*	5	36.2 ± 33.7	−18.3 ± 0.4	9.7 ± 0.3	3.50	2.69
Histioteuthis corona	4	42.3 ± 6.4	−18.1 ± 0.2	9.8 ± 0.6	3.53	3.91
Histioteuthis meleagroteuthis	8	50.1 ± 10.9	−18.2 ± 0.3	8.9 ± 0.8	3.50	3.66
Histioteuthis reversa	8,7	60.3 ± 50.1	−17.8 ± 0.2	11.4 ± 1.1	3.43	4.40
Stigmatoteuthis arcturi	3,4	31.8 ± 7.1	−18.6 ± 0.2	9.4 ± 0.7	3.50	3.81
Joubiniteuthidae						
_Joubiniteuthis portieri_*	5	60.7 ± 3.2	−17.1 ± 0.3	12.6 ± 0.3	3.44	3.55
Mastigoteuthidae						
_Mastigoteuthis agassizii_*	7	76.9 ± 16.4	−17.7 ± 0.2	13.5 ± 0.4	3.49	3.83
_Mastigopsis hjorti_*	3	63.0 ± 0	−17.5 ± 0.2	11.3 ± 1.5	3.45	3.18
_Mastigoteuthis magna_*	15	129.9 ± 75.5	−17.4 ± 0.3	12.7 ± 0.9	3.44	3.58
Octopoteuthidae						
Octopoteuthis sicula	14	74.6 ± 46.1	−17.8 ± 0.4	10.9 ± 2.3	3.71	4.25
Ommastrephidae						
Illex illecebrosus	4	256.3 ± 48.7	−17.8 ± 0.4	11.7 ± 0.8	3.41	4.49
Ommastrephes bartramii	6	138.8 ± 19.3	−17.6 ± 0.4	5.8 ± 0.7	3.54	2.75
Ornithoteuthis antillarum	11,7	49.9 ± 20.5	−19.0 ± 0.4	7.3 ± 0.6	3.53	3.19
Sthenoteuthis pteropus	11	75.2 ± 31.7	−18.9 ± 0.7	6.4 ± 0.7	3.45	2.92
Onychoteuthidae						
Onychoteuthis banksii	8,5	31.6 ± 14.5	−18.7 ± 0.1	7.2 ± 1.1	3.53	3.16
Pyroteuthidae						
Pyroteuthis margaritifera	8,2	24.0 ± 7.3	−18.8 ± 0.6	9.0 ± 0.2	3.32	3.68
Octopodiformes						
Argonautoidea						
Argonauta sp.[a]	9		−18.9 ± 0.3	8.6 ± 0.3	3.55	3.57
Haliphron atlanticus	11	88.4 ± 17.0	−18.0 ± 0.2	10.2 ± 0.3	3.67	4.02
Bolitaenidae						
Bolitaena pygmaea	6,4	37.8 ± 14.0	−18.3 ± 0.8	8.1 ± 0.9	3.60	3.43
Vampyroteuthidae						
_Vampyroteuthis infernalis_*	9	37.6 ± 19.5	−17.5 ± 0.3	12.0 ± 0.7	3.55	3.38

[a] No mantle length measurements were obtained for _Argonauta_ sp.

families Mastigoteuthidae (N = 1), Cranchiidae (N = 9) and Ommastrephidae (N = 4) were sampled at sizes ≥ 200 mm ML. Estimated trophic levels for these largest individuals in some cases were similar to values found in much smaller individuals from the same species.

A significant and positive relationship was observed between $\delta^{13}C$ values (N = 193) and mantle length ($R^2 = 0.10$, $F = 20.7$, $p < 0.001$), with larger individuals becoming more enriched in $\delta^{13}C$, suggestive of deeper foraging habitats with growth (Fig. 4B). Two outlier samples, both from the family

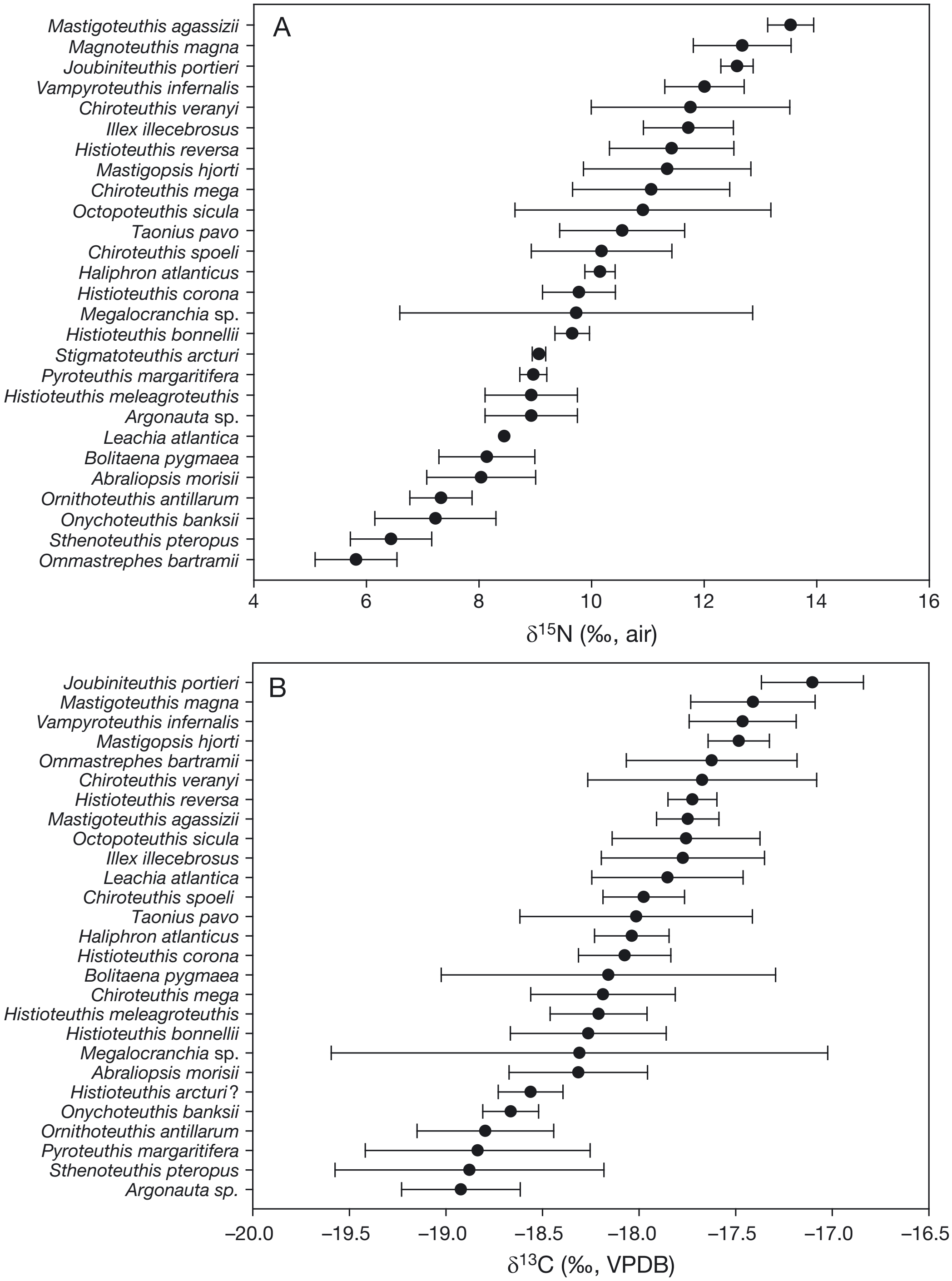

Fig. 2. Mean and standard deviations of stable (A) nitrogen and (B) carbon isotope values measured in the beaks of 27 cephalopod species from waters of the Bear Seamount

Cranchiidae (*Taonius pavo* and *Megalocranchia* sp.), exhibited relatively depleted carbon signals compared to other samples. The C:N ratios of these 2 samples were not exceptionally high (<3.8); therefore, it is unclear whether the isotopic signals from these individuals reflect true habitat use (more pelagic) or chitin-biased samples. Since these are the first reported isotope values of these species from the Northwest Atlantic, we chose not to exclude them from our results.

Top trophic positions within the overall assemblage (4.0 to 4.5) were held by *Illex illecebrosus*, *Histio-*

Table 2. Among-family differences in $\delta^{15}N$ and $\delta^{13}C$ (‰) values using a Kruskal-Wallis 1-way ANOVA on ranks and pairwise multiple comparisons tests (Dunns). Different letters show similarities and differences among families. SIBER analysis results show core isotopic trophic niche width (SEAc) and overall niche diversity (TA) measurements in beak tissues. Values correspond to Bayesian ellipses (SEAc) and convex hulls (TA) in Fig. 3B. ML: mantle length (mm). Bolitaenidae and Pyroteuthidae were excluded from SIBER analyses due to low paired sample sizes

Family	N	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	ML	SEAc	TA
Argonautoidea	20	D	F	88.4	0.71	1.74
Bolitaenidae	4	C	H	37.8	–	–
Chiroteuthidae	16	D	H	83.1	1.96	5.04
Cranchiidae	29	D	H	139.9	4.01	13.77
Enoploteuthidae	12	B	F	28.8	0.76	1.54
Histioteuthidae	27	D	H	45.3	1.21	3.67
Joubiniteuthidae	5	A	E	60.7	0.31	0.24
Mastigoteuthidae	25	A,C	E	110.9	1.03	2.77
Octopoteuthidae	14	D	G	74.6	2.96	5.25
Ommastrephidae	27	B	F	100.3	4.86	14.18
Onychoteuthidae	5	B	F, G	34.5	0.55	0.47
Pyroteuthidae	2	D	F, G	25.4	–	–
Vampyroteuthidae	9	A	E	37.6	0.70	1.03

teuthis reversa, *Octopoteuthis sicula*, *T. pavo*, and *H. atlanticus* (Table 1). Intermediate trophic positions (3.5 to 4.0) included several bathy/benthopelagic species *M. agassizii*, *M. magna*, *J. portieri*, and *Megalocranchia* sp., the histioteuthids *H. corona*, *H. meleagroteuthis* and *S. arcturi*, as well as *Pyroteuthis margaritifera*, and the pelagic octopod, *Argonauta* sp. The lowest trophic positions (2.7 to 3.4) included small ommastrephids, specifically juvenile *Ommastrephes bartramii*, *Sthenoteuthis pteropus*, and *Ornithoteuthis antillarum*, as well as *Onychoteuthis banksii*, *Histioteuthis bonnellii*, and *Abraliopsis morisii* (Table 1, Fig. 5B).

3.2. Isotopic niche width and overlap

Isotopic niche breadth (SEAc) and overall niche diversity (TA) ranged from 0.31 to 4.86 and from 0.4 to 14.18, respectively, across 11 cephalopod families. Isotopic niche breadth and diversity metrics were not significantly related to the number of species within each family unit (p-values > 0.08). Mean family values of isotopic niche breadth (R^2 = 0.43, *F* = 6.65, p = 0.03) and diversity (R^2 = 0.52, *F* = 9.58, p = 0.02) were positively related to mean mantle length. Cephalopod families exhibiting the narrowest isotopic niche breadth and niche diversity included Joubiniteuthidae, Onychoteuthidae, and Vampyroteuthidae (Fig. 3B). Conversely, the families Ommastrephidae, Cranchiidae, and Octopoteuthidae showed the broadest isotopic niches overall (Table 2; see Fig. A1 in

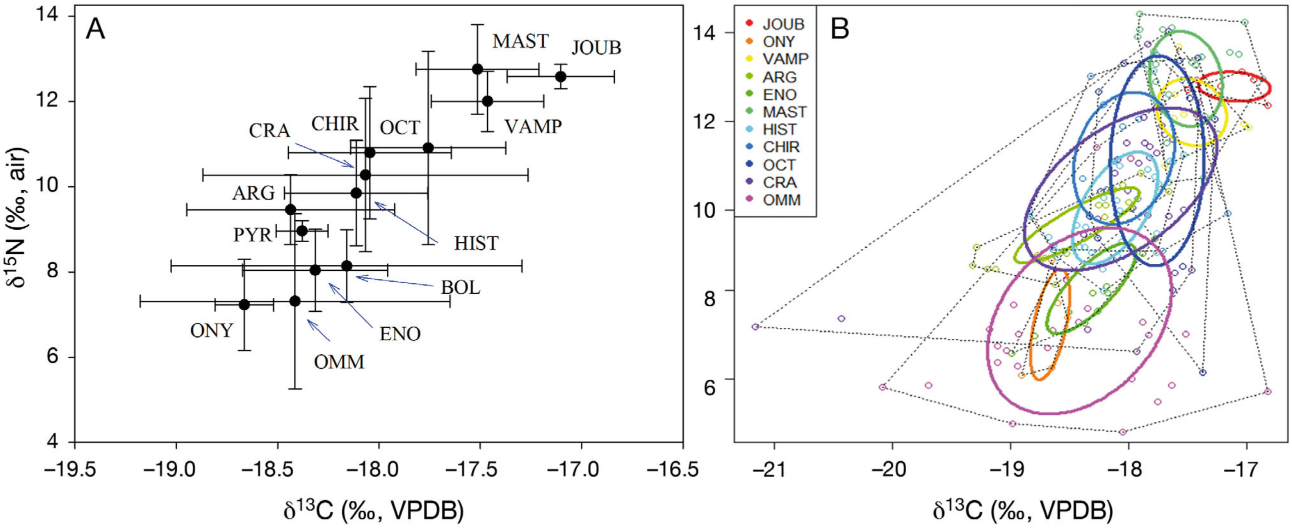

Fig. 3. Stable isotope (A) bi-plot and (B) SIBER ellipses of $\delta^{13}C$ (‰, VPDB) and $\delta^{15}N$ (‰, air) values for 13 cephalopod families from Bear Seamount. Bi-plots show mean ± SD for all individuals with paired measurements. Standard ellipses corrected for small sample sizes (SEAc) (solid lines) represent the core niche area of each family, and convex hulls of overall niche diversity (dotted lines) encompass all data points. In order of most enriched $\delta^{15}N$ values, Mastigoteuthidae (MAST), Joubiniteuthidae (JOUB), Vampyroteuthidae (VAMP), Octopoteuthidae (OCT), Chiroteuthidae (CHIR), Cranchiidae (CRA), Histioteuthidae (HIST), Argonautoidea (ARG), Pyroteuthidae (PYR), Bolitaenidae (BOL), Enoploteuthidae (ENO), Ommastrephidae (OMM), and Onychoteuthidae (ONY). Note that sample sizes were not large enough for Pyroteuthidae and Bolitaenidae to be included in the SIBER analysis

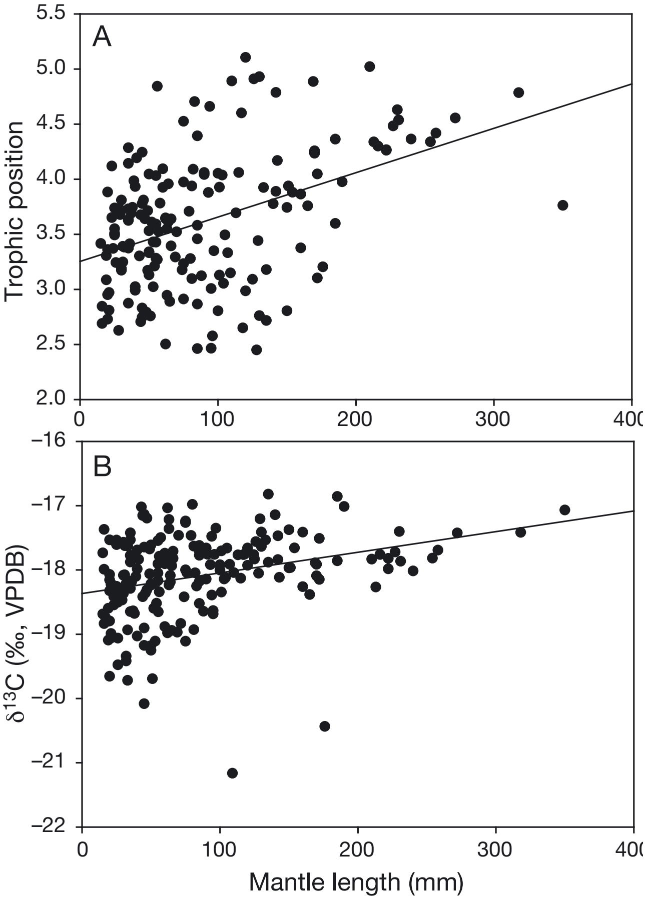

Fig. 4. Changes in (A) trophic position and (B) habitat use across the cephalopod assemblage of the Bear Seamount as a function of mantle length (ML). Note that only species with reliable measurements of ML (from relatively intact specimens) were included in this analysis

the Appendix). Overlap in SEAc values occurred to some extent for all but 5 family pair-wise combinations, and approximately a third of all groups shared relatively high isotopic niche space (overlap values ranged 20–39%) with another family (Table 3). Families with the largest isotopic niches (Ommastrephidae, Octopoteuthidae, Cranchiidae, and Chiroteuthidae) showed high overlap with each other (20–35%). The 3 bathy/benthopelagic families, Joubiniteuthidae, Mastigoteuthidae, and Vampyroteuthidae, occupied similar niche space, with overlap values ranging from 18 to 39%. Octopoteuthidae shared isotopic niche space with Mastigoteuthidae (25%), Vampyroteuthidae (19%) and to a lesser extent Joubiniteuthidae (7%). Joubiniteuthidae had the smallest and most unique (least amount of overlap: 0 to 22%) isotopic niche of all families evaluated. Ommastrephidae encompassed the isotopic niches of Argonautoidea, Onychoteuthidae and Enoploteuthidae (100%), and Cranchiidae completely overlapped the isotopic niche space of Histioteuthidae, Argonautoidea, Vampyroteuthidae, and Joubiniteuthidae (Table 3, Fig. 3B).

3.3. Within-family differences and species-specific ontogenetic shifts

Significant differences in δ^{15}N and δ^{13}C values were found among species within the families Ommastrephidae ($N_{species}$ = 4), Histoteuthidae ($N_{species}$ = 5), and Mastigoteuthidae ($N_{species}$ = 3) and the superfamily Argonautoidea ($N_{species}$ = 2) (Table 4, Fig. 6). Although data were available for multiple species within the families Chiroteuthidae and Cranchiidae (3 species in each family), significant differences were not found (p-values > 0.05). Within their respective family groups, *Illex illecebrosus* (Ommastrephidae), *Histioteuthis reversa* (Histioteuthidae), *Mastigoteuthis agassizii* (Mastigoteuthidae), and *Haliphron atlanticu*s (superfamily Argonautoidea) exhibited the highest δ^{15}N values and inferred trophic positions; *Histioteuthis reversa* and *Haliphron atlanticus* also exhibited significantly enriched carbon values compared to close relatives, potentially indicating different sources of primary productivity and thus habitat use within their respective groups (Table 4, Fig. 6).

Positive and significant ontogenetic shifts in δ^{15}N values with increasing body size were detected within the species *Abraliopsis morisii* (N = 12; R^2 = 0.52, *F* = 11.82, p = 0.006), *O. sicula* (N = 13; R^2 = 0.82, *F* = 54.04, $p < 0.0001$), *T. pavo* (N = 21; R^2 = 0.37, p = 0.0034), and multiple species from the family Ommastrephidae: *I. illecebrosu*s (N = 4, R^2 = 0.96, p = 0.022), *Ornithoteuthis antillarum* (N = 7, R^2 = 0.71, p = 0.02), *Ommastrephes bartramii* (N = 6, R^2 = 0.73, p = 0.03), and *Sthenoteuthis pteropus* (N = 11, R^2 = 0.60, p = 0.005) (Fig. 7). The only species from the family Histioteuthidae to show a significant ontogenetic shift was *Histioteuthis corona* (N = 4, R^2 = 0.99, p = 0.004), and δ^{15}N values declined with size; however, results were based on a relatively small sample size (N = 4) over a narrow range of mantle lengths and may not represent a true trend. Shifts in δ^{15}N values as a function of body size were tested but not significant in *H. reversa*, *H. bonnellii*, *H. meleagroteuthis*, *Stigmatoteuthis arcturi*, *Onychoteuthis banksii, C. mega, C. spoeli*, *Megalocranchia* sp., *M. agassizii*, *M. magna*, *B. pygmaea Haliphron atlanticus*, and *Vampyroteuthis infernalis*.

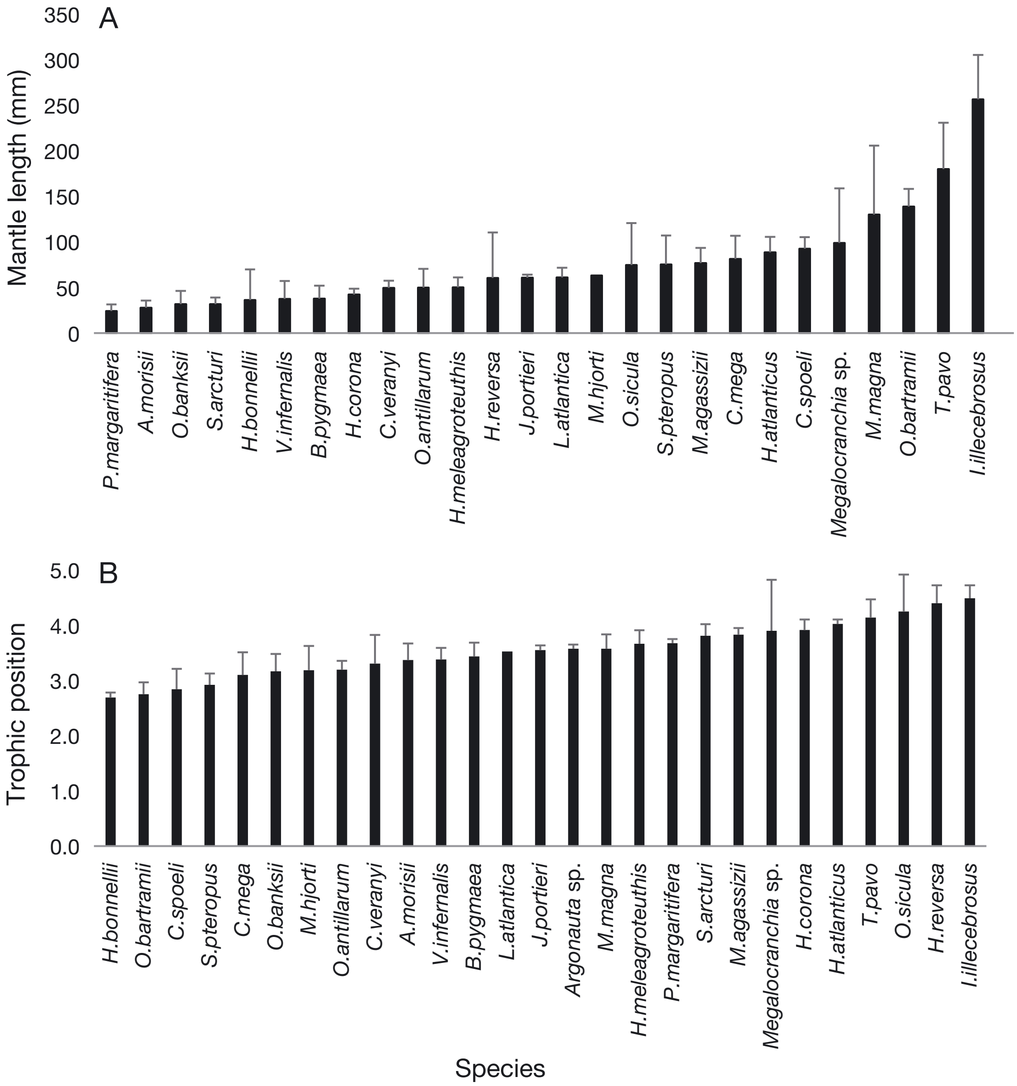

Fig. 5. Overall range of mean (±SD) species-specific values for (A) mantle length (mm) and (B) trophic position, ordered from smallest to largest

4. DISCUSSION

Stable isotope data from Bear Seamount quantify the trophic roles of approximately one-third of all deep-sea cephalopod species reported in temperate waters of the Northwest Atlantic Ocean (Shea et al. 2017) and provide the first description of the overall trophic structure of this guild. Specimens analyzed in this study primarily represent the integrated life history of juvenile and sub-adult life stages. Mean trophic positions spanned 1.8 levels across the 27 species and 13 families of cephalopods, ranging from 2.7 in *Histioteuthis bonnellii* to 4.5 in *Illex illecebrosus*. Individuals from multiple families and across a wide range of body sizes (30 to 350 mm ML) were often found to occupy similar trophic positions. The continuous gradient, relatively high overlap, and broad range of isotopic values across families, species, and body sizes suggests an unstructured assemblage comprised of generalist and specialist foragers distributed throughout a vertical depth range of midwater pelagic habitats (Miller et al. 2010, Madigan et al. 2012, Soares et al. 2014). These findings are similar to other cephalopod food webs documented in the Pacific and Northeast Atlantic but provide more nuanced trophic descriptions than have been reported previously (e.g. Cherel et al. 2009b, Madigan et al. 2012, Choy et al. 2015, Rosas-Luis et al. 2016, Merten et al. 2017).

Table 3. The percentage of shared isotopic niche space for all pair-wise comparisons of cephalopod families. Values in parentheses indicate the directional percent overlap of family A (column) with family B (row)

	Argonautoidea	Chiroteuthidae	Cranchiidae	Enoploteuthidae	Histioteuthidae	Joubiniteuthidae	Mastigoteuthidae	Octopoteuthidae	Ommastrephidae	Onychoteuthidae
Chiroteuthidae	20 (75, 27)									
Cranchiidae	15 (100, 18)	32 (97, 47)								
Enoploteuthidae	14 (29, 27)	17 (24, 62)	16 (18, 98)							
Histioteuthidae	27 (44, 74)	35 (56, 91)	23 (30, 100)	28 (72, 45)						
Joubiniteuthidae	0	8 (9, 56)	7 (8, 100)	0	5 (6, 23)					
Mastigoteuthidae	7 (18, 12)	25 (38, 73)	18 (23, 88)	<1 (2, 1)	15 (28, 33)	18 (78, 24)				
Octopoteuthidae	12 (62, 15)	35 (87, 57)	31 (55, 74)	14 (66, 17)	25 (86, 35)	7 (74, 8)	25 (98, 34)			
Ommastrephidae	13 (100, 15)	20 (70, 28)	30 (67, 56)	14 (100, 16)	19 (96, 24)	<1 (13, 1)	6 (36, 8)	24 (64, 39)		
Onychoteuthidae	13 (23, 30)	9 (11, 40)	9 (11, 77)	27 (46, 63)	18 (26, 56)	0	0	6 (7, 35)	10 (11, 100)	
Vampyroteuthidae	9 (18, 18)	23 (30, 86)	15 (17, 100)	<1 (2, 2)	18 (28, 48)	22 (72, 33)	39 (65, 97)	19 (23, 99)	7 (8, 55)	0

4.1. Isotopic niche overlap and breadth

Trophic similarity was high among approximately a third of all family members, though distinct trophic niches emerged on either end of the spectrum of nitrogen and carbon values. We expected groups known to undergo diel vertical migration to have wider isotopic niches and a broader range of carbon values representing multiple vertical habitat baselines, compared to non-migrators. This assumption held for a few families including Ommastrephidae, Cranchiidae and Chiroteuthidae, which exhibited the broadest isotopic niche areas and have varying vertical distribution patterns. However, Octopoteuthiidae had a broad overall isotopic niche, though they are found throughout the water column with no diel vertical migration pattern (Roper & Young 1975, H. Judkins & M. Vecchione pers. obs.).

Broad niches and high isotopic variability were observed at the family and species level in both very small (*Bolitaena pygmaea*), and very large-sized species (*Taonius pavo* and *Megalocranchia* sp.). These patterns either reflect ontogenetic shifts in foraging behavior or variation in isotopic baselines resulting from different habitat use in the early portions of

Table 4. Within family differences in isotopic values for a subset of groups with ≥3 species using 1-way ANOVA (*F*) or Kruskal-Wallis 1-way ANOVA (*H*) depending on whether the assumption of normality was upheld. Kruskal-Wallis test results are in **bold**. Different letters show results of pairwise multiple comparisons (Tukey Test) for parametric and (Dunns) for non-parametric tests. NS: non-significant within family differences

Family and species	$\delta^{13}C$ (‰) *F*, ***H***	$\delta^{13}C$ (‰) p	$\delta^{15}N$ (‰) *F*, ***H***	$\delta^{15}N$ (‰) p
Cranchiidae	**0.07**	NS	**1.85**	NS
Chiroteuthidae	2.04	NS	1.09	NS
Histioteuthidae	7.22	<0.001	**18.99**	<0.001
Histioteuthis bonnellii	B			
Histioteuthis corona	A, B, C			
Histioteuthis meleagroteuthis	B, C			
Histioteuthis reversa	A			
Stigmatoteuthis arcturi	C			
Mastigoteuthidae	3.62	0.04	6.15	0.003
Mastigoteuthis agassizii	A			
Mastigopsis hjorti	B			
Mastigoteuthis magna	A,B			
Ommastrephidae	9.9	<0.001	68.33	<0.001
Illex illecebrosus	A			
Ommastrephes bartramii	B			
Ornithoteuthis antillarum	C			
Sthenoteuthis pteropus	C, B			
Argonautoidea	61.84	<0.001	170.50	<0.001
Argonauta sp.				
Haliphron atlanticus				

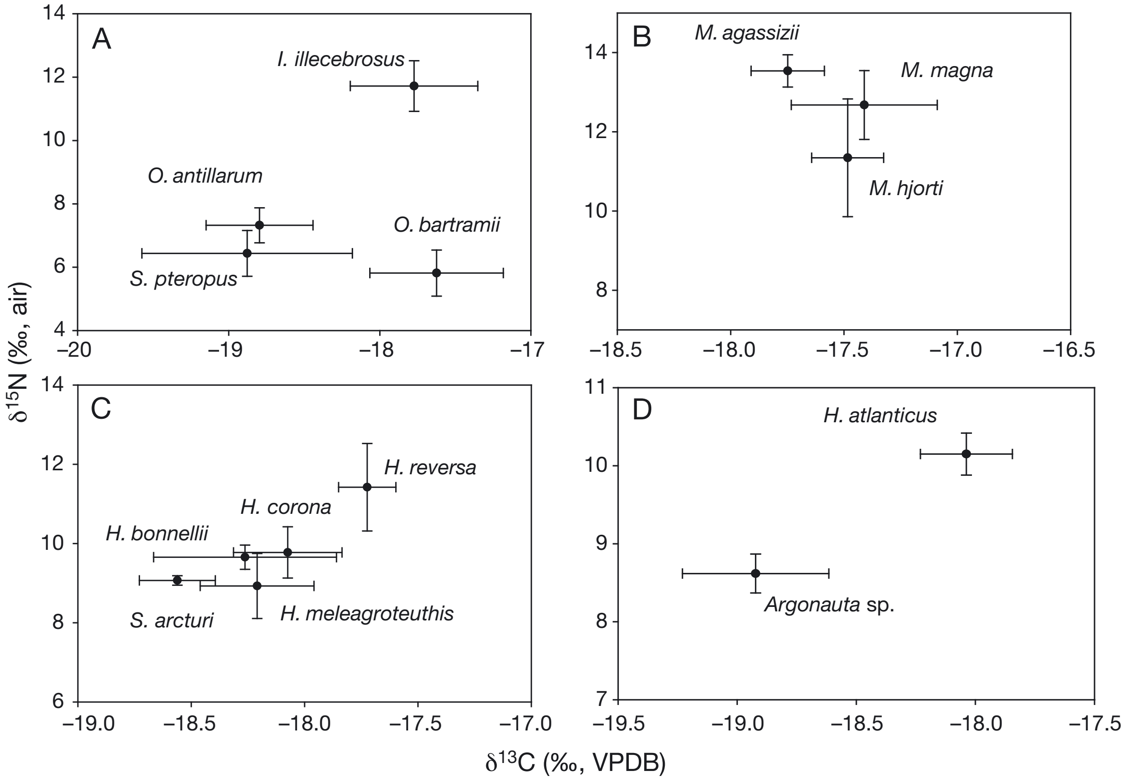

Fig. 6. Within-family stable isotope bi-plots of $\delta^{13}C$ (‰, VPDB) and $\delta^{15}N$ (‰, air) values for (A) Ommastrephidae, (B) Mastigoteuthidae, (C) Histioteuthidae, and (D) Argonautoidea. Bi-plots show mean ± SD. Note scaling on all axes varies with family group

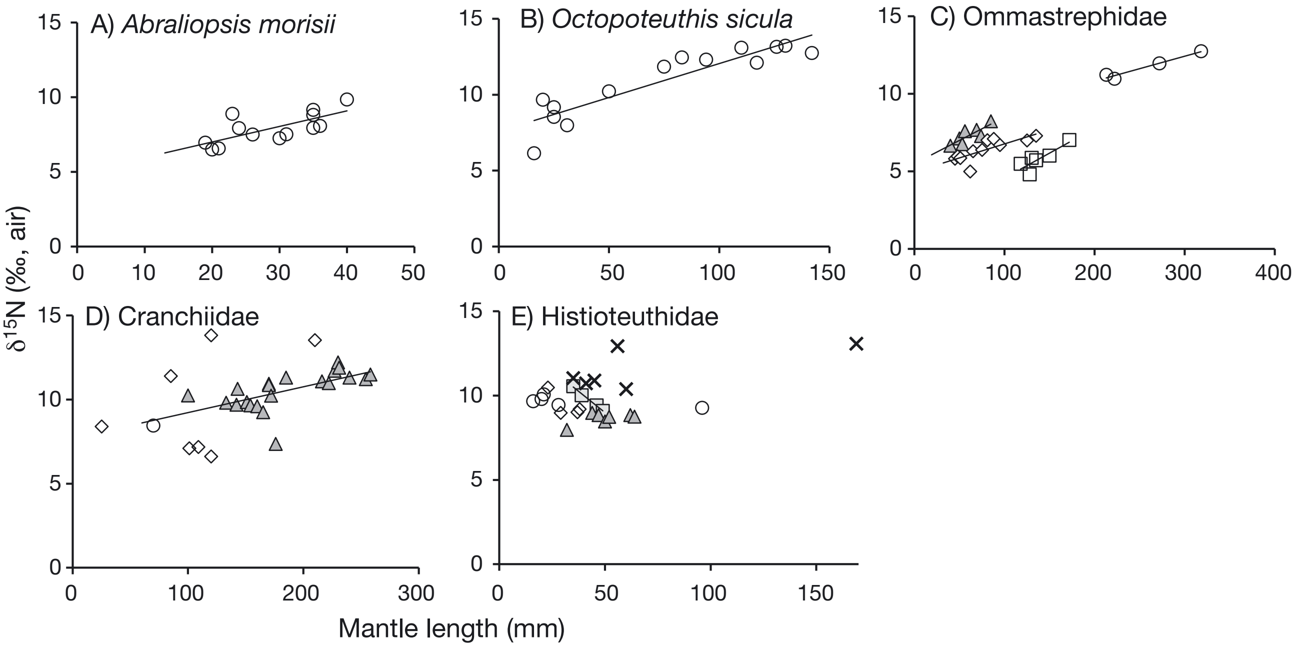

Fig. 7. Ontogenic shifts in $\delta^{15}N$ (‰, air) values as a function of mantle length (mm) were significant in the species (A) *Abraliopsis morisii*, (B) *Octopoteuthis sicula*, (C) 4 species within the family Ommastrephidae: *Illex illecebrosus* (circle), *Ommastrephes bartramii* (square), *Ornithoteuthis antillarum* (triangle), and *Sthenoteuthis pteropus* (diamond); (D) *Taonius pavo* (triangle), and (E) *Histioteuthis corona* (square). Data for additional species within the families Cranchiidae and Histioteuthidae are shown for context in (D) *Megalocranchia* sp. (diamond) and *Leachia atlantica* (circle), and (E) *H. reversa* (X), *H. bonnellii* (circle), *H. meleagroteuthis* (triangle), *Stigmatoteuthis arcturi* (diamond)

their lives. Ontogenetic shifts were demonstrated in *Octopoteuthis sicula* and *T. pavo*; however, trends were insignificant for other species within the Cranchiidae and Chiroteuthidae families, perhaps due to low sample sizes. Additional factors influencing niche breadth include opportunistic foraging on a range of nektonic prey as well as small sinking and suspended particles (Demopoulos et al. 2017, Gloeckler et al. 2018). Cannibalism is common in many species (Ibáñez & Keyl 2010, Choy et al. 2017), and there have been observations of squids feeding on prey of equal size or larger than themselves, which could also expand their trophic niche even at small body sizes (Rodhouse & Nigmatullin 1996).

Cephalopod families exhibiting the narrowest isotopic niche widths and overall diversity metrics at Bear Seamount included Joubiniteuthidae, Vampyroteuthidae, and Onychoteuthidae. Within these groups, the more gelatinous *Vampyroteuthis infernalis* does not rise above 600 m throughout its lifetime, and the more muscular squids, *Joubiniteuthis portieri* and small specimens of *Onychoteuthis banksii* are distributed throughout the water column with no vertical migration pattern (H. Judkins & M. Vecchione pers. obs.). While these species showed similar niche dimensions, the trophic niche of *O. banksii* was positioned much lower in the food web compared to the more bathy/benthopelagic species and showed more variation in δ^{15}N values. In the Gulf of Mexico, the diet of *O. banksii* includes copepods, euphausiids, and fishes (Passarella & Hopkins 1991). Little to nothing is known about the diet of *J. portieiri*, while *V. infernalis* has been characterized as having a passive feeding mode on detritus (Hoving & Robison 2012, Rosas-Luis et al. 2014). We hypothesize that the relatively narrow niche dimensions for these families are explained by a lack of diel vertical migration and occupation of distinct water masses through their integrated life history, which represents the period leading up to the juvenile and/or sub-adult phase. These isotopic patterns suggest they are specialists relative to other families at similar life stages in the Bear Seamount assemblage.

In the Monterey Submarine Canyon of the northeastern Pacific Ocean, *V. infernalis* is a non-migratory resident of low-oxygen (0.4 ml l^{-1}) pelagic waters (Hoving & Robison 2012). To the best of our knowledge, stable isotope analyses have not been published on specimens from this area; however, in the eastern Atlantic, *V. infernalis* was found to have some of the most depleted isotopic values of all cephalopods observed (Cherel et al. 2009b). This is in stark contrast to the relatively enriched δ^{15}N values and intermediate trophic position estimated for *V. infernalis* at Bear Seamount. Emerging research has shown *V. infernalis* consume other cephalopods when given the opportunity (B. A. Siebel unpubl. data) and may not be a strict detritovore as previously thought (Hoving & Robison 2012). Our findings suggest significant regional ecological differences may exist for *V. infernalis*, possibly due to the lack of a physiologically important oxygen-minimum zone in the Northwest Atlantic and different baseline conditions inherent in various ocean basins. A multi-ocean basin comparative approach using a combination of gut content analysis, metabarcoding of stomach contents, and compound-specific stable isotopes would be useful to resolve potential ecological differences in *V. infernalis* across its global range (McMahon et al. 2016).

Some of the smallest squids (17−85 mm) evaluated in this study included the muscular vertically migrating enoploteuthid, pyroteuthid, and ommastrephid squids *Abraliopsis morisii, Pyroteuthis margaritifera*, and *Ornithoteuthis antillarum.* It was somewhat surprising that these species occupied lower or equivalent trophic positions to that of gelatinous species (e.g. *B. pygmaea*, *Leachia atlantica*), which are generally assumed to be more passive foragers (Gloeckler et al. 2018). Muscular body types and swimming abilities lead to the assumption that these squids should be capable of hunting and capturing mobile mid-trophic level prey, such as fishes and other cephalopods, even at small body sizes. Enoploteuthids, such as *A. morisii* and *P. margaritifera*, remain relatively small throughout their lives (maximum ML = 45 mm) (Jereb & Roper 2010) feeding primarily on copepods, euphausiids, other small invertebrates, and to a lesser extent small fishes and cephalopods (Passarella & Hopkins 1991). Isotopic niche areas show an ontogenetic shift for *A. morisii*, but insufficient nitrogen data were recovered from beak samples in *P. margaritifera* to make any inferences. For the early to mid-life stages represented in our evaluations, these squids appear to be primarily tracking and consuming lower trophic level prey (e.g. zooplankton) as they migrate vertically in the water column. It is possible that these species could be utilizing habitats with different isotopic baselines that confounded estimations of trophic positions. Few studies have described the isotopic structure of deep-sea habitats of the Northwest Atlantic (Logan & Lutcavage 2013, Oczkowski et al. 2016, Demopoulos et al. 2017); therefore, high uncertainty exists for fine scale habitat use and trophic relationships.

Ommastrephid squids occupied the broadest of all isotopic niches and had high trophic redundancy with several other midwater families. They are active predators, foraging throughout the water column as they migrate on a diurnal basis, consuming a mixture of crustaceans, fishes such as myctophids, and other cephalopods (Boyle & Rodhouse 2005). Relative amounts of prey consumed varies by ommastrephid species, region, and season, with juveniles generally consuming more crustaceans than older life phases (Lipiński & Linkowski 1988, Dawe et al. 1997, Dawe & Brodziak 1998, Watanabe et al. 2004, Parry 2006). Interestingly, the 2 large squids *I. illecebrosus* and *Ommastrephes bartramii* occupied vastly different trophic positions. In the Southwest Atlantic, *O. bartramii* have been shown to be cannibalistic as well as consuming histioteuthids, enoploteuthids, and argonauts (Lipiński & Linkowski 1988). The diet of *I. illecebrosus* is primarily known from specimens captured in shelf waters but also indicates high levels of cannibalism as well as predation on inshore fishes and the longfin inshore squid *Doryteuthis pealeii* (Maurer and Bowman 1985, Cargnelli et al. 1999), the latter likely not being representative of the diet of the population living in deep water environments of Bear Seamount. *Ommastrephes bartramii*, *S. pteropus*, and *O. antillarum* attain body sizes much larger than were evaluated here (Jereb & Roper 2010). Conversely, large (>200 mm ML) *I. illecebrosus* were some of the few adult specimens evaluated at Bear Seamount and reveal new details on the offshore component of the population, which is quite poorly known (Dawe et al. 1997, Dawe & Brodziak 1998, Cargnelli et al. 1999).

Based on results in other ocean basins (Takai et al. 2000, Golikov et al. 2018), additional sampling of larger, mature individuals across many Bear Seamount species is expected to reveal more pronounced ontogenetic shifts, higher trophic levels, and expanded isotopic niche breadths than were measured here. Additional studies that analyze multiple beak structures (e.g. rostrum, wing, and lateral walls) would be useful to reconstruct distinct portions of the trophic history and resolve remaining uncertainties (Cherel & Hobson 2005, Parry 2006, Cherel et al. 2009a, Guerra et al. 2010, Queirós et al. 2018).

4.2. Conflicting patterns in body size and isotopic enrichment

Mantle length was a good overall predictor of trophic level across the cephalopod community at Bear Seamount, but there was substantial variation in the range of body sizes representing high and low trophic positions at the individual and species level. For example, some of the species that grow large (e.g. *Ommastrephes bartramii*) on average occupied some of the lowest trophic positions. Individual body size is usually a better indicator of trophic position within a community, more so even than species (Jennings & Reynolds 2007), and this pattern held true for cephalopods at Bear Seamount. However, in deep-sea habitats, a range of factors can confound the relationship between body size and trophic position when patterns are interpreted using $\delta^{15}N$ values.

In the Northwest Atlantic and other ocean basins, it is well known that $\delta^{15}N$ values become enriched with depth due to bacterial remineralization of particulate organic matter and the upwelling of nutrient-rich bottom waters from slope environments (Mintenbeck et al. 2007, Oczkowski et al. 2016, Demopoulos et al. 2017, Richards et al. 2019). Relatively enriched $\delta^{15}N$ values were characteristic of bathy/benthopelagic species from the families Chiroteuthidae, Mastigoteuthidae, Vampyroteuthidae, and Joubiniteuthidae caught at Bear Seamount. Individuals were not particularly large, are weakly muscular to gelatinous, and do not possess morphological characteristics consistent with that of active searching predators (Hoving & Robison 2012). When estimating trophic position, we accounted for the influence of nitrogen enrichment with depth by using a deep-sea benthic species as a baseline (Demopoulos et al. 2017), which would otherwise have resulted in elevated trophic positions for these species where it may not have been ecologically warranted. It is certainly possible that other species within the assemblage at Bear Seamount could also be influenced by deep or multiple isotopic baselines occurring across the depth zones sampled (up to ~1900 m); however, we did not have sufficient information to assign many cephalopod species with confidence to more narrowly defined depth zones and corresponding isotopic baseline. Nonetheless, there is emerging evidence that organisms distributed throughout epipelagic, mesopelagic and some bathypelagic habitats are supported by surface production that is either consumed and transported to depth by vertically migrating prey or fast-sinking particles (Richards et al. 2019). Additional constraints included assumptions of a constant trophic enrichment factor (TEF) in our calculations of trophic position and a fixed chitin correction factor to account for beak to tissue conversions, which may not be appropriate for all species; however, specific fractionation rates are not readily available for deep-sea species (Post 2002, Demopoulos et al. 2017). Our results were based on bulk stable isotope analysis, which is not able to fully differentiate among sources of production from the surface and particulate organic matter suspended at deeper depths. Future work using compound-specific stable isotopes would help clarify fine-scale trophic and spatial differences within this and other deep-sea food webs (Demopoulos et al. 2017, Richards et al. 2019).

4.3. Trends in cephalopod biodiversity and abundance relative to trophic roles

Cephalopods documented at Bear Seamount during 2012 represent a year of relatively high biodiversity and abundance compared to the long-term series conducted between 2000 and 2014 (Shea et al. 2017). Six of the 27 species collected during 2012 and evaluated in the present study, *Mastigoteuthis agassizii*, *Magnoteuthis magna*, *V. infernalis*, *I. illecebrosus*, *Histioteuthis reversa*, and *T. pavo,* were persistent (found during all 8 cruises) and numerically dominant (comprising 75% of all specimens caught) over the 14 yr sampling period at Bear Seamount. These species are common prey to medium and large cetaceans, such as sperm whales *Physeter macrocephalus*, long-finned pilot whales *Globicephala melas*, pygmy *Kogia breviceps* and dwarf *K. sima* sperm whales in the Atlantic Ocean (Clarke et al. 1993, Gannon et al. 1997, Spitz et al. 2011, Staudinger et al. 2014), as well as large pelagic fishes and sharks (Staudinger et al. 2013). These species appear to be present in high numbers during a substantial portion of the annual cycle, possibly year-round, and are an essential part of the regional food web both as midwater consumers and as food to apex predators of high conservation and management concern. It is also noteworthy that specimens of *Haliphron atlanticus* collected in 2012 were among the largest ever collected at Bear Seamount. The anomalous diversity, abundance, and body sizes of cephalopods observed during this year could be the result of unique oceanographic conditions characterized by the warmest year in the Northwest Atlantic Ocean since the 1980s and a notably strong NAO Index (Mills et al. 2013, Oczkowski et al. 2016). Water and chlorophyll samples collected on the continental shelf also showed regional primary productivity rates were elevated and higher than average δ^{13}C values were present during 2012 (Oczkowski et al. 2016). These anomalous conditions likely affected isotopic signatures in cephalopod tissues, and future studies in the region will be useful to compare results across average and extreme years to determine how cephalopod biodiversity and trophic roles may vary accordingly.

4.4. An evolving understanding of cephalopod trophic ecology

Differences in isotopic baselines make direct comparisons with other regions problematic; however, some insights can be gained into how cephalopod trophic roles may vary or be similar between regions based on relative positions and overall isotopic ranges within their respective food webs. High overlap among families, high intra-family variability, and increasing trophic position with growth were consistent findings for cephalopods at Bear Seamount and specimens obtained from large pelagic fish diets in nearby habitats of the central North Atlantic (Logan & Lutcavage 2013). Trophic diversity was similar at Bear Seamount and in the Bay of Biscay in the Northeast Atlantic, where 19 cephalopod species spanned a narrower range of isotope values, covering 1.5 trophic levels (Cherel et al. 2009b). In slope waters of the Kerguelen Islands of the Southern Ocean, 18 cephalopod species consumed by teleost, seabird, and elasmobranch predators spanned a continuum of 3 trophic levels (Cherel & Hobson 2005).

Because of our poor understanding of deep-sea systems, it is unclear how much of the variation observed in cephalopods across regions is due to differences in trophic roles or collection methods. Specimens were caught at Bear Seamount using standardized survey gear, which has some inherent limitations. Large muscular taxa as well as delicate gelatinous taxa may be under-represented due to their ability to outswim and avoid nets or because they are badly damaged by sampling gear. For example, *Argonauta* sp. are rarely captured in midwater nets, yet they are one of the most commonly recovered octopods in the diets of regional large pelagic fishes and are believed to be a key component of offshore food webs (Staudinger et al. 2013). In comparison, most other studies that have documented deep-sea cephalopod trophic ecology to date have used specimens obtained from the stomachs of marine mammals, seabirds and large pelagic fishes (Clarke 1996, Jackson et al. 2007, Logan et al. 2011, Logan & Lutcavage 2013, Staudinger et al. 2014, Seco et al. 2016, Xavier et al. 2018). While information gained from using predators as biological samplers has advanced our understanding of cephalopod diversity and biogeography, results may represent biased selections of species and body sizes that are dependent on predator foraging behavior (e.g. diving depth) and selective abilities (e.g. mouth gape) (Staudinger et al. 2013, Young et al. 2010). The use of beak tissues for analysis in the present study, rather than soft tissues (e.g. mantle), was deliberate and part of a long-term sampling strategy for assessing the ecosystem role of deep-sea cephalopods that takes into account their catchability by direct (i.e. surveys) and indirect (i.e. predator stomachs) sources.

An emerging finding across recent studies is that cephalopods occupy a wider range of trophic roles than previously thought (Cherel & Hobson 2005, Navarro et al. 2013, Golikov et al. 2018). In many systems, particularly offshore habitats, the trophic niches of cephalopods consistently overlap with top predators (Cherel et al. 2009b, Logan et al. 2011, Madigan et al. 2012, Logan & Lutcavage 2013, Navarro et al. 2013). Studies in waters near Bear Seamount have shown the diets of large pelagic fishes (e.g. tunas and dolphinfish) can comprise substantial amounts of epipelagic and mesopelagic cephalopods but exhibit similar and sometimes lower δ^{15}N values than some of the cephalopods examined here (Teffer et al. 2015). In addition, regional studies of deep-diving kogiid whales that forage almost exclusively on mesopelagic squids exhibited δ^{15}N values similar to their primary prey (Histioteuthidae, Ommastrephidae, and Cranchidae) (Staudinger et al. 2014). Although multiple baselines may be confounding these results (Chouvelon et al. 2012), these results challenge previous assumptions that as invertebrates, cephalopods should be restricted to low to mid trophic levels. Ecosystem models of the Northwest Atlantic (e.g. Ecopath) commonly group all squids together regardless of size and species (Morissette et al. 2006, 2009, Zhang & Chen 2007). Depending on the diversity of cephalopods present in a region, these models may be underestimating trophic redundancy, oversimplifying the guild and failing to accurately depict the breadth of trophic roles represented in a given food web. This can result in decreased estimates of ecosystem stability and poor overall understanding of resilience to environmental and anthropogenic stressors, such as climate change and fishing pressure (Madigan et al. 2012). Cephalopods are increasingly being recognized as a key forage resource (National Coalition for Marine Conservation; Lenfest Forage Fish Task Force), yet additional attention is still needed to capture and resolve the full range of their potential functional ecology as competitors as well as mid- to high-level predators.

In conclusion, this study provides novel information on a wide range of deep-sea cephalopods — an important taxonomic group in global oceans; however, many questions remain unresolved. A multifaceted approach using a range of observational and molecular techniques is perhaps the only way we will be able to ascertain the full breadth of trophic roles and delineate separate but inter-locked vertical foodwebs of deep-sea cephalopods. Ideally, data from predator diets, survey gear, and *in situ* feeding observations from remotely operated vehicles (Choy et al. 2017) would be integrated with molecular tools such as metabarcoding and compound-specific stable isotopes to resolve isotopic baselines, to clarify food habits and to obtain sufficient samples on poorly known species. Simultaneous sampling and/or comparisons with apex predators would also help resolve whether trophic positions of cephalopods, large pelagic fishes and marine mammals are truly equivalent or influenced by different (e.g. deep vs. surface water) δ^{15}N baselines. Nonetheless, emerging information on the spectrum and diversity of ecological roles within the cephalopod group is compelling and deserves more attention in the future.

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Appendix

Table A1. Summary of midwater trawls conducted during the 2012 National Marine Fisheries Service biodiversity cruise (ID# PC1205) on the NOAA ship ‘Pisces’. Latitude and longitude indicate the coordinates at which each tow began. NA: net did not deploy correctly on those tows; a maximum depth was not determined but specimens were collected. Date is given as mo/d in 2012

Date	Depth / time of day	Bottom /midwater	Latitude	Longitude	Maximum depth of net (m)
8/30	Shallow / day	Midwater	39.94	–67.28	602
8/30	Deep / day	Midwater	39.92	–67.28	1921
8/31	Shallow / night	Midwater	39.93	–67.27	688
8/31	Shallow / night	Midwater	39.93	–67.25	1220
8/31	Shallow / day	Midwater	39.78	–67.41	969
8/31	Deep / day	Midwater	39.78	–67.43	1520
9/1	Shallow / night	Midwater	39.75	–67.45	802
9/1	Deep / night	Midwater	39.74	–67.48	1066
9/1	Shallow / day	Midwater	39.90	–67.61	614
9/1	Deep / day	Midwater	39.93	–67.71	1290
9/2	Shallow / night	Midwater	39.91	–67.62	750
9/2	Deep / night	Midwater	39.96	–67.57	1313
9/2	Shallow / day	Midwater	40.04	–67.48	964
9/2	Deep / day	Midwater	40.11	–67.42	1354
9/3	Shallow / night	Midwater	40.05	–67.47	870
9/3	Deep / night	Midwater	40.08	–67.38	1332
9/3	Deep / day	Bottom	39.95	–67.46	NA
9/3	Deep / day	Bottom	39.95	–67.46	1297
9/4	Shallow / day	Midwater	39.95	–67.46	790
9/4	Deep / day	Midwater	39.95	–67.58	1461
9/5	Shallow / night	Midwater	39.93	–67.44	NA
9/5	Shallow / night	Midwater	39.95	–67.45	1052
9/5	Shallow / day	Midwater	39.94	–67.40	1000
9/6	Deep / night	Midwater	39.74	–67.49	1217
9/6	Deep / night	Midwater	39.80	–67.51	1314
9/6	Deep / day	Midwater	39.69	–67.57	1447
9/6	Deep / day	Midwater	39.79	–67.54	1446
9/7	Deep / night	Midwater	39.78	–67.53	1525
9/7	Deep / night	Midwater	39.76	–67.50	1788

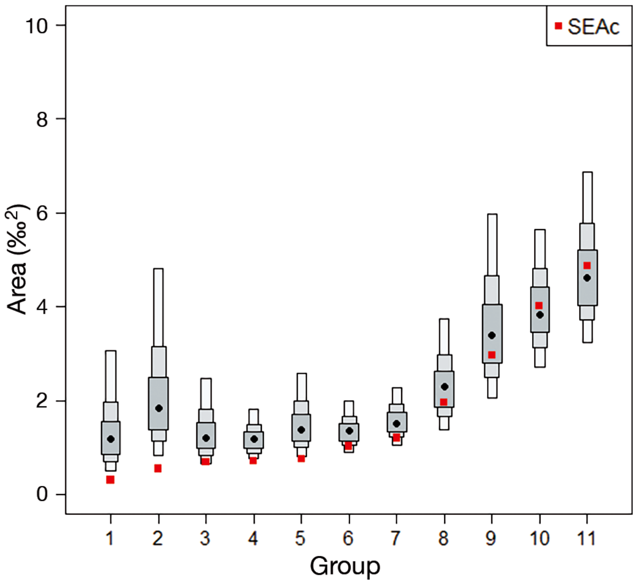

Fig. A1. Density plot showing the confidence intervals of the standard ellipse areas. Black round points correspond to the mean standard ellipse area, red square points to the SEAc, and gray shaded boxed areas reflect the 9 %, 75 %, and 50 % confidence intervals from lightest to darkest, respectively. Cephalopod families are ordered from smallest to largest SEAc values and correspond to Table 5: Joubiniteuthidae (JOUB), Onychoteuthidae (ONY), Vampyroteuthidae (VAMP), Argonautoidea (ARG), Enoploteuthidae (ENO), Mastigoteuthidae (MAST), Histioteuthidae (HIST), Chiroteuthidae (CHIR), Octopoteuthidae (OCT), Cranchiidae (CRA), Ommastrephidae (OMM)

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