

Food-web dynamics and isotopic niches in deep-sea communities residing in a submarine canyon and on the adjacent open slopes

Amanda W. J. Demopoulos^{1,*}, Jennifer McClain-Counts¹, Steve W. Ross²,
Sandra Brooke³, Furu Mienis⁴

¹US Geological Survey Wetland and Aquatic Research Center, Gainesville, FL 32653, USA

²University of North Carolina, Wilmington, NC 28409, USA

³Florida State University, St. Teresa, FL 32358, USA

⁴Royal Netherlands Institute for Sea Research, Den Burg 1790, The Netherlands

ABSTRACT: Examination of food webs and trophic niches provide insights into organisms' functional ecology, yet few studies have examined trophodynamics within submarine canyons, where the interaction of canyon morphology and oceanography influences habitat provision and food deposition. Using stable isotope analysis and Bayesian ellipses, we documented deep-sea food-web structure and trophic niches in Baltimore Canyon and the adjacent open slopes in the US Mid-Atlantic Region. Results revealed isotopically diverse feeding groups, comprising approximately 5 trophic levels. Regression analysis indicated that consumer isotope data are structured by habitat (canyon vs. slope), feeding group, and depth. Benthic feeders were enriched in ¹³C and ¹⁵N relative to suspension feeders, consistent with consuming older, more refractory organic matter. In contrast, canyon suspension feeders had the largest and more distinct isotopic niche, indicating they consume an isotopically discrete food source, possibly fresher organic material. The wider isotopic niche observed for canyon consumers indicated the presence of feeding specialists and generalists. High dispersion in $\delta^{13}\text{C}$ values for canyon consumers suggests that the isotopic composition of particulate organic matter changes, which is linked to depositional dynamics, resulting in discrete zones of organic matter accumulation or resuspension. Heterogeneity in habitat and food availability likely enhances trophic diversity in canyons. Given their abundance in the world's oceans, our results from Baltimore Canyon suggest that submarine canyons may represent important havens for trophic diversity.

KEY WORDS: Stable-isotope analysis · Food web · Deep sea · Niche breadth · Slopes · Submarine canyon · US mid-Atlantic

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INTRODUCTION

Understanding food webs and resource partitioning between organisms is fundamental to ecology, providing insight into ecosystem function. Describing an organism's ecological niche, defined as the sum of an organism's interactions within its environment (both abiotic and biotic) (Hutchinson 1957, 1978), can provide insights into species' coexistence,

competition for resources, and the overall stability of communities (McGill et al. 2006). A trophic or dietary niche represents a subset of an organism's ecological niche, and is influenced by the diversity of resources available to consumers and associated trophic interactions (Elton 1927, Musseau et al. 2015). Characterizing trophic niches is a well-established approach to understanding the dietary ecology of organisms and communities (Elton 1927). Defining dietary niches by

examining prey diversity and nutritional resources (Peterson et al. 2011) helps elucidate an organism's functional role in food webs (Musseau et al. 2015), including the presence of dietary specialists and generalists. Trophic niche specificity is influenced by many factors, including species' morphology and habitat specificity, where niche specificity may help reduce interspecies competition in food-poor (quality, quantity) areas and/or when resources are ephemeral (Iken et al. 2001, Sherwood et al. 2008).

In the deep sea, consumers' energetic requirements rely on particulate flux raining from surface waters (Gage & Tyler 1991, Klages et al. 2003). However, the deep sea is generally a food-limited environment because only a small percentage of particulate organic carbon (POC) produced in surface waters settles to the seafloor (Gage & Tyler 1991, De La Rocha & Passow 2007). Transport of carbon to the seafloor occurs through numerous processes including vertical flux of phytodetritus produced in surface waters, lateral transport, and through diel vertical migrators, including zooplankton, cephalopods, and fishes (Inthorn et al. 2006, Trueman et al. 2014). Deposited POC promotes feeding and reproduction by benthic communities, influencing overall carbon cycling in the ocean (Gage & Tyler 1991). In particular, channeling and deposition of organic matter (OM) in deep-sea canyons, which are functions of canyon morphology, can enhance benthic productivity (Duineveld et al. 2001), leading to high biodiversity and biomass (Vetter & Dayton 1998, 1999) and trophic complexity (Stefanescu et al. 1994, Cartes & Sorbe 1999, Cartes et al. 2010, Romero-Romero et al. 2016). Therefore, hydrological and geomorphological processes influencing the supply and resuspension of POC to canyon environments, rather than depth-related food-limitation, may drive trophic structure, community composition, and biodiversity in submarine canyons (Dell'Anno et al. 2013).

Continental margins are incised by numerous submarine canyons, with approximately 6000 found globally between 200 and 3000 m (De Leo et al. 2010). Canyons often experience dynamic flow and turbulence, in contrast to more quiescent areas of the margin. Habitat heterogeneity is characteristic of submarine canyons, including steep and rugged topography and variable substrate types; this complexity influences access to food resources (e.g. quality, quantity) and diversity of biological communities (McClain & Barry 2010). Internal tides can promote mixing near the seafloor leading to sediment resuspension, while other regions within canyons are characterized by accumulation of material (Masson

et al. 2010), which can influence food availability to canyon and slope consumers. However, the few studies that have compared the trophic ecology of canyon and adjacent slope invertebrate and fish communities were often limited in depth range, spatial scale, or taxonomic composition and richness (Cartes & Sorbe 1998, Schmiedl et al. 2000, Duineveld et al. 2001, Bianchelli et al. 2008, Cartes et al. 2010, 2014, Mamouridis et al. 2011, Fanelli et al. 2013, Papiol et al. 2013, Romero-Romero et al. 2016).

Stable isotope analysis (SIA) can help unravel complex food webs, particularly in the remote deep sea. Stable carbon isotopes ($\delta^{13}\text{C}$) closely reflect a consumer's food source (DeNiro & Epstein 1978, Wada et al. 1991), while stable nitrogen isotopes ($\delta^{15}\text{N}$) are used to approximate trophic level (TL) (Minagawa & Wada 1984, Post 2002). The stable isotopic composition of sinking OM changes with depth due to preferential assimilation of the light isotopes during microbial metabolism (Mintenbeck et al. 2007). On continental slopes, slow deposition of particulate organic matter (POM) dominates, leading to enriched isotopic composition due to ongoing microbial degradation (Mintenbeck et al. 2007). In contrast, within canyon environments, upwelled, nutrient-rich water enhances surface primary production, and hydrodynamics induce rapid transport, deposition, and resuspension of this fresh OM (Bosley et al. 2004). Hence, within canyons, rapidly sinking particles may experience less fractionation (Rau et al. 1991), potentially resulting in depleted ^{13}C and ^{15}N values relative to the older, more refractory, OM found on the adjacent open slopes. Biological processing within the benthos can also result in higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, leading to enriched isotope values with every TL. Given key differences in habitat heterogeneity, depositional environments and corresponding food availability to the benthos, we hypothesized that canyon and slope food webs differ in their reliance on fresh, ^{13}C -depleted OM versus older, ^{13}C -enriched OM.

The quality and availability of OM utilized by deep-sea benthos influences the development of different trophic niches, which can be examined using SIA (Iken et al. 2001, Jeffreys et al. 2009, Fanelli et al. 2013, Tecchio et al. 2013, Reid et al. 2016). SIA estimates of food-chain length and TL provide temporally and spatially integrated trophic estimates used to define trophic niches at the species and community level (France et al. 1998, Jennings et al. 2001, Davenport & Bax 2002, Harvey et al. 2002, Al-Habsi et al. 2008). Isotopic niche space represents the relative position of individuals, populations, and communities in bivariate isotope space, e.g. $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$

(Jackson et al. 2011, Layman et al. 2012), which can yield insights into food resource use. Examining overlap in isotopic niches can help understand niche specialization, while isotopic niche size and width among communities or within assemblages estimate trophic diversity (Layman et al. 2007). Given the potential for diverse food resources to be present within dynamic canyon environments resulting from complex resuspension and deposition regimes, isotopic niches among canyon consumer groups may differ. Specific questions regarding trophic niches in the canyon environments include (1) what are the sizes of isotope niches based on feeding group type (e.g. suspension vs. benthic feeders)? Also, (2) do canyon environments promote higher trophic diversity (e.g. several niches and large niche breadth), or trophic redundancy (e.g. species with overlapping trophic niches) compared to adjacent slopes?

In this study, we used SIA and isotope niche width analysis to characterize food web structure and trophic niches in a US mid-Atlantic canyon and the adjacent slopes. Given that habitat heterogeneity and OM supply and quality available to the benthos may differ between canyons and slope environments, we hypothesized that canyon consumers have differ-

ent isotopic compositions and wider isotopic niches than consumers on the adjacent slopes. Ultimately, examining food web structure can help identify mechanistic drivers of diversity patterns and community function within these environments (Bianchelli et al. 2008, Cartes et al. 2010).

MATERIALS AND METHODS

Study location

Baltimore Canyon, situated along the US Atlantic margin, 100 km offshore of Maryland, has distinct resuspension (200 to 600 m, down to 800 m) and deposition zones (>900 m; Gardner 1989a,b, F. Mienis et al. unpubl. data) that are composed of organic-poor and organic-rich sediments, respectively. In contrast, the slopes adjacent to Baltimore Canyon are characterized by relatively uniform sediment deposition, with decreasing organic content with depth, which is typical for deep-sea environments. Sampling was conducted within Baltimore Canyon and on the adjacent slopes (Fig. 1) during 4 research cruises from 2011 to 2013 (see Table S1 in the Supplement at

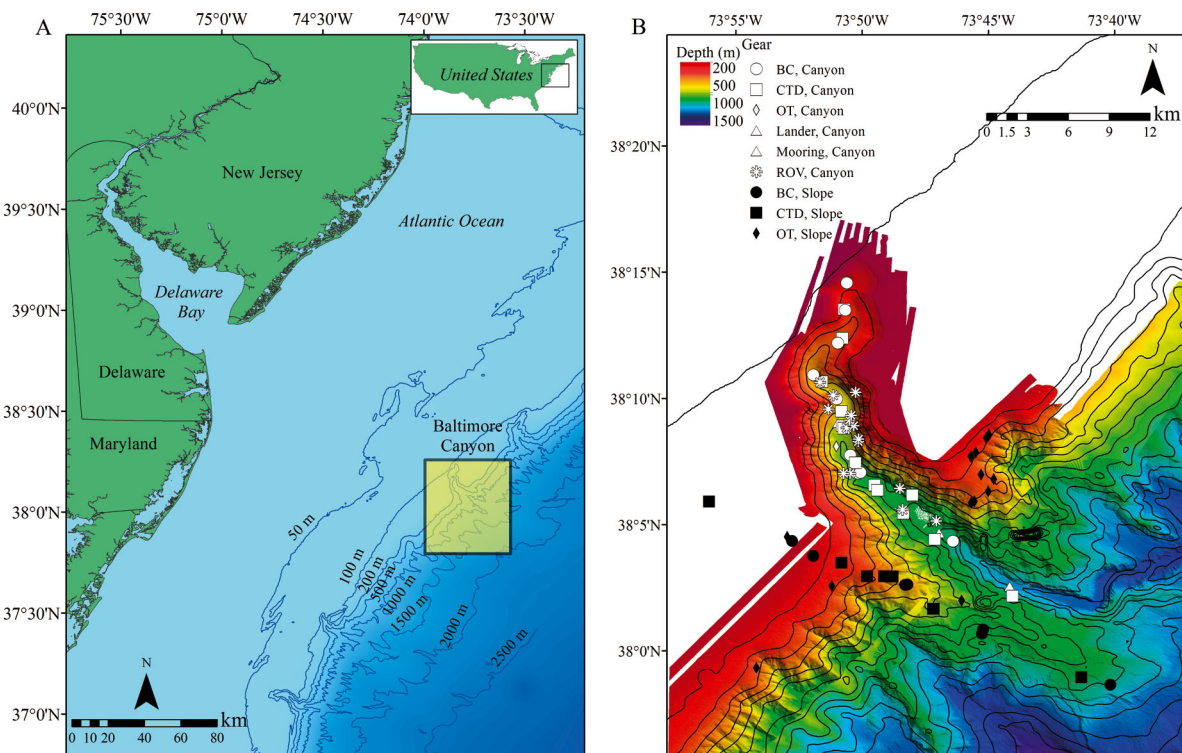


Fig. 1. (A) Bathymetry of the continental shelf off the northeast United States in the mid-Atlantic Ocean. Baltimore Canyon and adjacent slope (yellow box) were sampled from 2011 to 2013. (B) Multibeam data of Baltimore Canyon with symbols representing the different types of gear (BC: box core; CTD: conductivity, temperature, depth rosette with Niskins; OT: otter trawl; ROV: remotely operated vehicle) used to sample particulate organic matter (POM), fauna, and sediments for stable isotope analyses from the canyon (white symbols) and the adjacent slopes (black symbols)

www.int-res.com/articles/suppl/m578p019_supp.pdf). Details on the geomorphology of this region's canyons were documented by Obelcz et al. (2014).

Sampling methods

Collections were conducted using the NOAA ships 'Nancy Foster' and 'Ron Brown' and remotely operated vehicles (ROVs) 'Kraken II' (2012) and 'Jason II' (2013). Multiple gear types, including otter trawls, box cores, ROV push cores, ROV suction, and Niskin bottles were used to sample fauna, suspended POM, and sediments. Otter trawls (4.9 m head rope, 38.1 mm mesh), were deployed and towed for ~30 min at ~2 knots (3.7 km h⁻¹) ground speed to sample benthic fauna. Sediment samples were collected using a Royal Netherlands Institute for Sea Research (NIOZ)-designed box corer with a cylindrical core tube (30 cm diameter, 55 cm height) deployed from the ship. Smaller tube cores (31.65 cm² × 30 cm) were inserted into each box core to subsample sediments for analyses. Water samples were collected at various depths using Niskin bottles mounted on a CTD rosette. Fauna were collected using either the suction systems or the manipulator arms on the ROVs, while sediments were collected using push cores (31.65 cm² × 30 cm) operated by the ROV manipulator arm. Additional water samples were collected using Niskin bottles attached to the ROV. Bottom water was collected within 10 m of the seafloor and surface seawater was collected within 10 m of the surface. Sediment trap samples were collected using 2 Technicap PPS 4/3 sediment traps and a Honjo Parflux sediment trap programmed to rotate on a 30 d interval at 3 depths within the canyon: 603, 1082, and 1318 m. Sediment trap samples were divided into 5 equal splits with a rotor splitter at NIOZ. Two splits were rinsed, frozen, freeze-dried, and prepared for isotope analysis.

Dissections of fish and invertebrate tissues occurred prior to preservation. For consistency, tissue was removed from similar body regions based on taxa (e.g. muscle from the dorsal region of fishes, caudal tissue of shrimps, leg muscle for crabs, mantle, gill and adductor muscle for molluscs, legs for brittle stars, gonads for urchins, and polyps for corals). Tissue samples were dried to a constant weight at 50 to 60°C, ground to a fine powder and weighed into tin capsules. Invertebrate samples were acidified with 10% platinum chloride to remove inorganic carbon. POM filters were dried and both filters and sediment trap material were treated with 1.0 N

hydrochloric acid, then transferred into tin boats. Sediment samples were homogenized prior to drying and acidified with 1.0 N phosphoric acid before weighing into tin boats.

Samples (tissue, sediment, POM) were processed as in Demopoulos et al. (2008) and analyzed for δ¹³C and δ¹⁵N composition referenced to Vienna PeeDee Belemnite and atmospheric nitrogen, respectively. Analyses were conducted at Washington State University using a Costech elemental analyzer interfaced with a GV instruments Isoprime isotope ratio mass spectrometer. Isotope ratios were expressed as δ¹³C and δ¹⁵N, in per mil (‰). Reported δ¹³C values were taken from analyzed acidified samples and δ¹⁵N values from non-acidified samples to avoid the potential artefact associated with acidification (Pinnegar & Polunin 1999). Precision and accuracy examined through replicate analysis of laboratory standards were <0.2‰ in C and N (Demopoulos et al. 2008). Specific laboratory standards used included bovine liver, albumin, and acetanilide. Data were examined for potential lipid contribution and for samples that had C:N values >3.5, their corresponding δ¹³C values were mathematically corrected for the effect of lipid concentration on δ¹³C measurements using the methods of Post et al. (2007) for invertebrates and Hoffman & Sutton (2010) for fishes. Following the correction, the δ¹³C values were compared using paired *t*-tests; differences between the pairs were significant for both fishes (*t* = -17.27, *df* = 288, *p* < 0.001, mean difference = -0.59) and invertebrates (*t* = -34.028, *df* = 509, *p* < 0.001, mean difference = -0.88). Ten samples had C:N values >8 and were excluded from analysis as per recommendations from Hoffman & Sutton (2010).

Data analysis

Trophic levels were calculated as follows:

$$TL_{\text{consumer}} = [(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{hydrozoan}}) / 3.4] + 2 \quad (1)$$

where δ¹⁵N values from hydrozoans were used to represent the baseline primary consumer present in canyon (δ¹⁵N = 7.4 ± 0.7‰) and slope (δ¹⁵N = 4.8 ± 0.4‰) environments. We assumed the trophic enrichment factor (TEF) of ¹⁵N to be 3.4 ± 0.98‰ SD, consistent with assumptions implicit to previous food-web studies (Post 2002, Vander Zanden & Fetzer 2007). Calculated TL errors incorporated the errors for all terms in the equation.

All data presented represent untransformed means (±1 SE). Bottom-water POM and sediment stable iso-

tope data were compared using a 1-way analysis of variance (ANOVA). All data were tested for normality and heteroscedasticity using Shapiro-Wilk and Levene's tests (Zar 1999). If data were not normally distributed, then a non-parametric Kruskal-Wallis (KW) test was used, followed by post hoc pairwise Wilcoxon tests.

Feeding group assignments (infaunal, epibenthic, suprabenthic, deposit, pelagic, suspension, benthic, benthic/pelagic, deposit/suspension, and unknown) and definitions were based on literature review (see Table S2 in the Supplement). Feeding groups were defined as follows: infaunal feeders consumed material living in sediments, epibenthic feeders grazed on surface of sediment, suprabenthic feeders ate fauna living in close proximity and interacting with the benthos, and benthic feeders included multiple consumer categories (any combination of infauna, epibenthic or suprabenthic). Pelagic feeders were mobile fauna that consumed prey in the water column. Benthic/pelagic feeders fed on taxa associated with the seafloor and the water column. Deposit feeders consumed organic material settled on sediment, including detritus. Suspension feeders were sessile, attached fauna that consumed material suspended in water column, not directly associated with benthos. Deposit/suspension feeders consumed both

deposited and suspended organic material. A few taxa could only be classified as unknown feeding group, due to the lack of species-specific taxonomic resolution (e.g. shrimp spp.).

Ordinary least squares (OLS) regression was used to investigate whether there were habitat (canyon vs. slope), depth, and/or feeding group differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using the base functions in R (R Core Team 2016). We built several model sets (Table 1), by first constructing a null model which estimated the mean with no predictors. Subsequent models increased complexity by adding 1 co-variate at a time, including habitat, depth, and feeding group, and second-order polynomials of each variable as additive or interactive terms. Model validation was undertaken by assessing normality and homogeneity of variance of the residuals of the best-fitting model by examining the following plots: quantile–quantile plots, histograms of standardized residuals, plots of standardized residuals versus fitted values, and box-plots of standardized residuals per habitat, depth, and feeding group. Akaike's information criterion (AIC_c) was used to assess the relative goodness of fit using the 'MuMIn' R package (Barton 2016). The model with the lowest AIC_c value was judged to be the best fitting model unless the difference between AIC_c (ΔAIC_c) was < 2 . When ΔAIC_c val-

Table 1. Ordinary least squares (OLS) model selection tables based on consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values where habitat = canyon or slope, and group = feeding group. AIC_c = Akaike's information criterion. Models ranked by $\text{AIC}_c(x)$

$\delta^{13}\text{C}$ models	df	AIC_c	ΔAIC	Adjusted r^2	$\delta^{15}\text{N}$ models	df	AIC_c	ΔAIC	Adjusted r^2
Habitat \times group \times depth ²	48	2196.6	0	0.66	Habitat \times group \times depth ²	48	3324.4	0	0.57
Habitat \times group \times depth	33	2252.7	56.09	0.63	Habitat \times group \times depth	33	3343.1	18.65	0.55
Habitat + group \times depth	18	2298.0	101.37	0.61	Habitat + group \times depth	18	3414.3	89.88	0.50
Habitat \times group	17	2331.0	134.39	0.59	Group \times depth	17	3479.5	155.05	0.46
Habitat \times group + depth	18	2331.3	134.72	0.59	Habitat \times group + depth ²	19	3513.0	188.55	0.44
Habitat \times group + depth ²	19	2333.4	136.81	0.59	Group \times depth ²	18	3528.4	203.99	0.43
Group \times depth	17	2365.7	169.10	0.57	Habitat \times group + depth	18	3531.6	207.14	0.42
Group \times depth ²	18	2389.3	192.68	0.56	Habitat + group + depth ²	12	3550.0	225.56	0.41
Habitat + group	10	2418.1	221.56	0.54	Habitat \times depth + group	12	3560.9	236.45	0.40
Habitat \times depth + group	12	2418.7	222.09	0.54	Habitat + group + depth	11	3562.4	237.95	0.40
Habitat + group + depth	11	2419.1	222.51	0.54	Habitat \times group	17	3624.2	299.82	0.36
Habitat + group + depth ²	12	2419.8	223.19	0.54	Group + depth ²	11	3625.1	300.64	0.35
Group + depth ²	11	2471.2	274.59	0.51	Group + depth	10	3629.9	305.49	0.35
Group + depth	10	2473.2	276.61	0.51	Habitat + group	10	3655.7	331.26	0.33
Group	9	2493.8	297.17	0.50	Group	9	3671.8	347.34	0.31
Habitat \times depth ²	6	2809.1	612.48	0.27	Habitat \times depth ²	6	3753.6	429.16	0.24
Habitat \times depth	5	2815.2	618.60	0.27	Habitat + depth ²	5	3763.8	439.40	0.23
Habitat + depth	4	2827.3	630.69	0.26	Habitat + depth	4	3773.3	448.84	0.22
Habitat + depth ²	5	2828.5	631.89	0.26	Habitat \times depth	5	3775.3	450.85	0.22
Habitat	3	2828.6	631.99	0.26	Habitat	3	3900.6	576.14	0.10
Depth ²	4	3049.9	853.32	0.04	Depth ²	4	3959.8	635.37	0.03
Depth	3	3051.8	855.25	0.03	Depth	3	3961.4	636.98	0.03
Null model	2	3078.8	882.19	0.00	Null model	2	3985.9	661.50	0.00

ues are <2 , then both models have similar validity (Reid et al. 2016). We plotted the best-fit model results (including 95% confidence envelopes) and raw isotope data ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) versus depth to illustrate how well the model fit the spread of isotope data for each feeding group. In order to address if the isotope samples were spatially independent, we ran an autocorrelation analysis in R using non-parametric spline correlograms, fit using the function 'spline.correlog' from the package 'nfc' (Bjørnstad & Falck 2001, Bjørnstad 2016).

Sample size-corrected standard ellipse area (SEA_c), the Bayesian SEA (SEA_B), ellipse metrics (eccentricity, E ; and the angle theta, θ), and SEA_c overlap were calculated using the SIAR and SIBER packages (Jackson et al. 2011, Reid et al. 2016) in R version 3.2.4 (R Core Team 2016) for major taxa and feeding groups separated into canyon and slope groups. SEA_c is the population isotopic niche, size-corrected to avoid issues that stem from small sample sizes. For the SIBER analysis, feeding groups were classified under the 'group' category and canyon and slope habitats were classified under the 'community' category. SEA_B was calculated from 10^4 posterior iterations of SEA_B based on the dataset, resulting in a range of SEA_B probability values, and we reported the mode with 95% credible intervals. The SEA_B illustrated the total amount of niche space occupied by the 'community' (i.e. canyon or slope), or 'group' (i.e. feeding group), and can be used to approximate the extent of the trophic diversity and utilized resources. E is a function of the variance on the x - and y -axes (e.g. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively): low E will have similar variance on both axes, appearing circular, whereas high E values will be a more elongated ellipse, either in the x or y direction. θ values ranged between 0 and π , reported here in degrees between 0 and 180. Values close to 0 represent relative dispersion along the x -axis ($\delta^{13}\text{C}$), consistent with consumers using multiple resources or source mixing. In contrast, for θ values close to 90° , the ellipse is spread along the y -axis ($\delta^{15}\text{N}$), consistent with groups feeding across different trophic positions within uniform basal carbon sources. Positive θ indicates that both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are directly proportional, whereas negative θ indicates that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are inversely proportional.

SIBER was used to investigate the structure of the food webs (Jackson et al. 2011) using the following Layman metrics (Layman et al. 2007): $\delta^{13}\text{C}$ range (CR), $\delta^{15}\text{N}$ range (NR), mean distance to centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of nearest neighbor distance

(SDNND). NR estimates food-web length, where a larger range among consumers suggests more trophic levels and higher trophic diversity. CR represents the width of the food web serving as a metric for trophic diversity, with higher values indicating multiple basal sources that may facilitate niche diversification at the base of the food web. CD is an estimate of trophic diversity within a food web, and is a function of the degree of species spacing, providing an indirect estimate of trophic redundancy (i.e. number of taxonomically distinct species that exhibit similar ecological functions) (Layman et al. 2007). MNND and SDNND serve as metrics of trophic redundancy, where small MNND values correspond to food webs with a high proportion of species that have similar trophic ecologies (higher trophic redundancy) (Layman et al. 2007, Saporiti et al. 2015). Low SDNND values reflect a more even distribution of trophic niches.

To test the sensitivity of SEA_c , SEA_B , θ , and E to differences in the number of individuals within the different feeding groups, isotope data across feeding groups were randomly reduced by 40%, with the exception of infauna feeders (canyon), which only had 5 individuals. To test if the analysis was sensitive to the isotope values of particular taxa, data were reduced by the number of taxa (5 or 10) within each feeding group, with the exception of the feeding groups that had 5 or fewer distinct taxa (deposit, epibenthic, infaunal, suprabenthic, and unknown for canyon; deposit, epibenthic, and unknown for slope). Estimates for SEA_c , SEA_B , θ , and E from these simulations were compared to the full model. Deposit/suspension and benthic/suspension feeding groups were removed from the OLS, SIAR, and SIBER analyses due to insufficient sample sizes ($n < 5$) and the unknown group only included shrimp spp. for the analyses.

RESULTS

A total of 1013 samples, representing 8 phyla, were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Stable isotope data indicated the main carbon source for all specimens was derived from photosynthetic material (-22.9 to -15.5‰ ; Fig. 2, Table S3 in the Supplement). POM collected near the seafloor (bottom POM) was enriched in ^{15}N compared to surface POM for both canyon and slope environments. Stable carbon and nitrogen isotope values for the sediment traps deployed within the canyon were within the range of POM and sediment isotope values, and were very consistent across sam-

pled depths ($\delta^{13}\text{C}$: -22.4 to -22.3% ; $\delta^{15}\text{N}$: 4.8 to 4.9%). There were no significant differences between canyon and slope $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for bottom POM ($\delta^{13}\text{C}$: KW, $\chi^2 = 0.278$, $p = 0.598$; $\delta^{15}\text{N}$: ANOVA, $F = 0.909$, $p = 0.355$), or sediment (ANOVA: $\delta^{13}\text{C}$, $F = 0.3545$, $p = 0.5572$; $\delta^{15}\text{N}$, $F = 3.405$, $p = 0.077$). Canyon sediments were significantly enriched in ^{13}C and depleted in ^{15}N relative to canyon bottom POM ($\delta^{13}\text{C}$: KW, $\chi^2 = 12.778$, $p = 0.0003$; $\delta^{15}\text{N}$: ANOVA, $F = 9.564$, $p = 0.005$). Likewise, slope sediment was enriched in ^{13}C relative to slope bottom

POM (ANOVA, $F = 19.282$, $p = 0.001$), but there was no difference in $\delta^{15}\text{N}$ between these 2 primary sources (ANOVA, $F = 3.475$, $p = 0.085$).

Stable isotope results revealed that the canyon and slope communities were composed of several feeding groups (Fig. 2, Table S3), occupying approximately 4 to 5 TLs. Canyon consumers were generally depleted in ^{13}C and ^{15}N relative to consumers on the adjacent slopes (Fig. S1). Suspension feeders were depleted in both isotopes compared to organisms feeding on benthic resources (Figs. 2

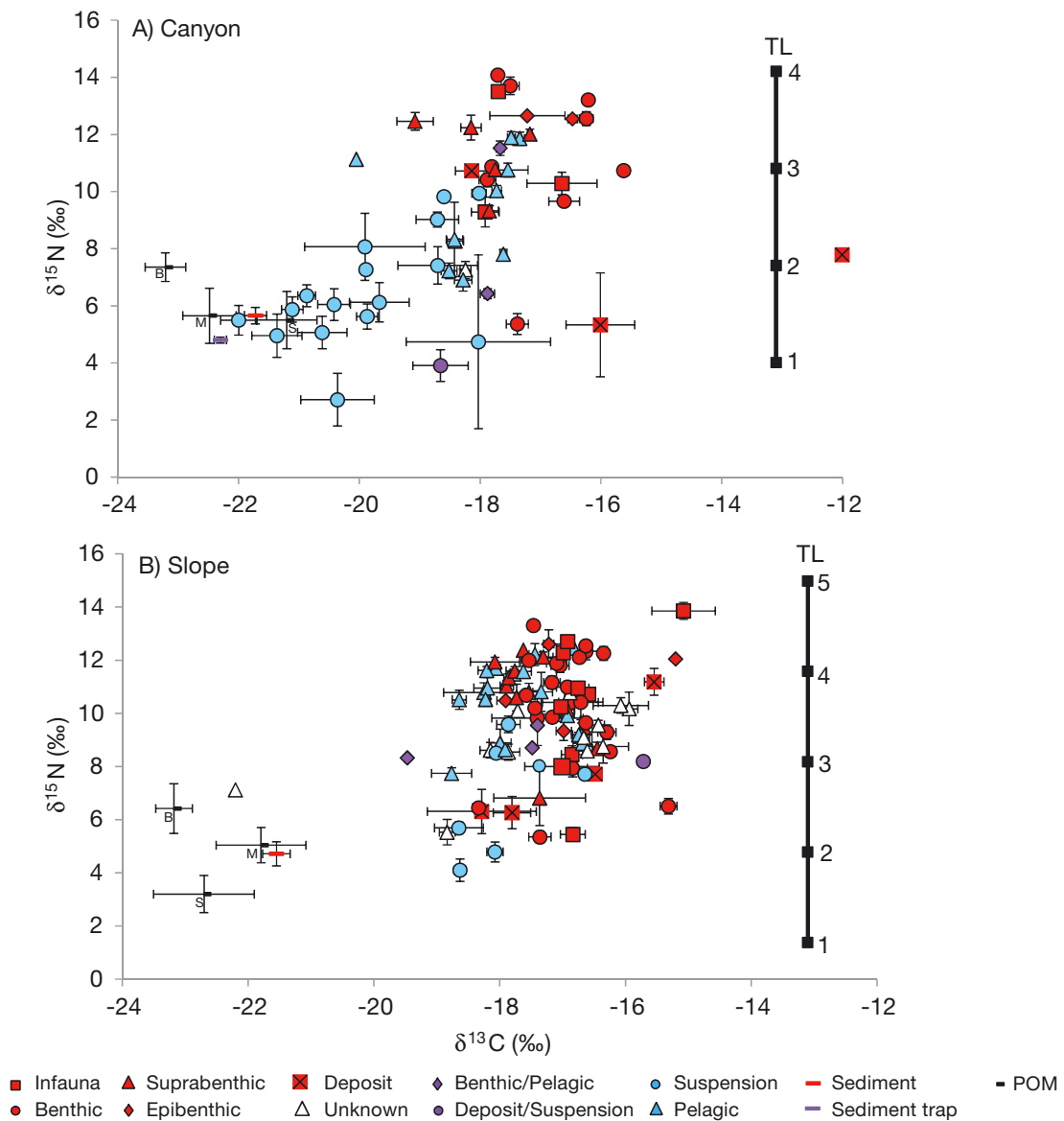


Fig. 2. Average $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values ($\% \pm 1$ SE) for particulate organic matter (POM) (B: bottom; M: midwater; S: surface), consumers, sediment traps (average of all data), and surface sediments (0 to 2 cm) collected from (A) Baltimore Canyon and (B) on adjacent slope. Colors represent general feeding strategies; red: benthos; blue: water column; purple: mixed diets. Symbols represent different feeding groups. Trophic level (TL) bar illustrates calculated trophic position (1 to 5) (see 'Materials and methods')

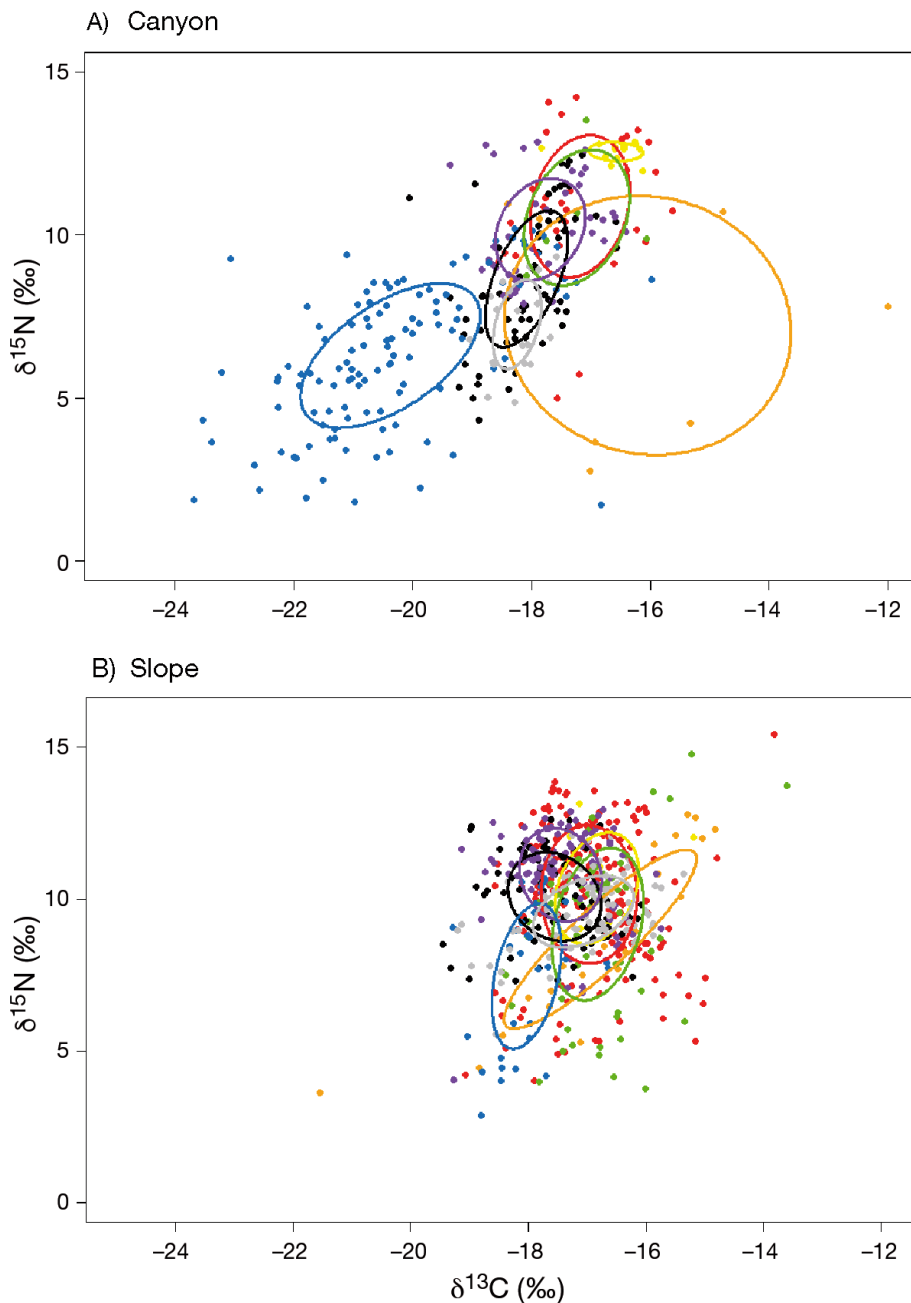


Fig. 3. Raw stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; ‰) from (A) Baltimore Canyon and (B) slope fauna and standard ellipse area (SEA_c) for each feeding group. Values of the SEA_c ellipse areas are included in Table 3. Ellipses and dots correspond to the following feeding groups: blue: suspension; black: pelagic; red: benthic; orange: deposit; yellow: epibenthic; green: infauna; purple: suprabenthic; grey: unknown

& 3), and unknown feeders were intermediate between benthic and suspension feeders. Several cnidarians and a few echinoderms occupied the lowest TL (~2), with fishes and an unidentified asteroid representing the highest order consumers (TL 4 to 5) (Fig. 2).

OLS model results

The fully interactive model, which included habitat (canyon or slope), feeding group, and a quadratic term for depth was the best model to explain the variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 1), explaining 66% of the variation in $\delta^{13}\text{C}$ and 57% in $\delta^{15}\text{N}$. Examination of the residuals from the top models revealed no spatial autocorrelation for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Fig. S2). Model-fitted data of depth versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values provided the best fit for benthic, pelagic, and suspension feeders for both canyon and slope fauna (Figs. S3–S5). The model provided a good fit for suprabenthic fauna from the slope only (Fig. S6); however, it was less reliable for the other feeding groups (Figs. S7–S10). $\delta^{13}\text{C}$ values for benthic feeders decreased slightly with depth in canyon, then increased at deeper depths, whereas $\delta^{15}\text{N}$ values increased with depth for both slope and canyon fauna (Fig. S3). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for pelagic feeders increased with canyon depth, whereas $\delta^{13}\text{C}$ values declined with depth on the slope (Fig. S4). For suspension feeders, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values initially declined with depth for both canyon and slope environments, then isotope values increased at deeper depths (greater than ~800 m) within the canyon. In contrast, at depths greater than ~500 m, the slope model was less reliable for suspension feeders, with greater separation observed in the model-fitted confidence envelopes (Fig. S5).

Isotope niche area estimates

Canyon fauna had longer food chains (NR) and higher trophic diversity (CR) compared with fauna from the adjacent slope (Table 2). The higher CD values estimated for canyon fauna indicates higher

Table 2. Mean probability values of Layman metrics for Baltimore Canyon and slope food webs. Canyon-specific values in **bold** were significantly higher ($p < 0.01$) than corresponding slope metrics. NR: $\delta^{15}\text{N}$ range; CR: $\delta^{13}\text{C}$ range; CD: mean distance to centroid; NND: nearest neighbor distance; SDNND: standard deviation of nearest neighbor distance

	Canyon	95 % CI	Slope	95 % CI
NR	6.26	5.63 to 6.92	3.35	3.07 to 3.92
CR	4.33	3.60 to 5.21	1.25	0.90 to 1.98
CD	2.11	2.03 to 2.45	0.92	0.82 to 1.06
NND	1.32	1.03 to 1.47	0.63	0.53 to 0.80
SDNND	0.78	0.60 to 1.07	0.48	0.26 to 0.71

trophic diversity is reflected at multiple trophic levels and a high degree of species spacing. Lower MNND and SDNND for slope consumers indicated evenness in their isotope values and a high degree of trophic redundancy and overlap of their feeding niches.

Community-wide SEA_c values were higher for canyon (11.67% ; Fig. S1) than for the adjacent slopes (5.84%). Cnidaria and Echinodermata had higher SEA_c and SEA_B values compared to the same groups on the slope (Table S4). In contrast, other decapods (non-shrimp spp.) had higher SEA_B on the slope. SEA_B values for fishes, shrimp spp., and Euphausiacea did not differ between the 2 environments. Amphipoda, Annelida, Mollusca, and Salpida were excluded from the between-taxa comparisons due to insufficient sample sizes. Examination of the standard ellipse areas in relationship to the raw isotope data (Fig. 3) revealed that both SEA_c and SEA_B estimates differed by feeding group pairs (Table 3, Fig. 3). SEA_B values for canyon consumers were less than the adjacent slope for epibenthic and unknown groups. In contrast, SEA_B values were greater in the canyon for deposit and suspension feeders. Ellipse overlap was high for all groups except epibenthic, unknown, and suspension feeders. Canyon suspension feeders had distinct SEA_c and SEA_B values, separate from all other groups (Fig. 3). Within this feeding group, canyon corals had larger SEA_B (4.20) values than canyon

anemones (1.71), with zero overlap, indicative of corals having a distinct isotopic niche compared to anemones.

Qualitative comparisons of the ellipse metrics E and θ indicated spatial differences in the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for certain feeding groups, consistent with the OLS results. E and θ values for benthic consumers were similar in canyon and slope habitats, with ellipses primarily stretched along the y -axis ($\delta^{15}\text{N}$; Fig. 3, Table 3). Suspension feeders from the slope had higher E and θ values than those from the canyon, illustrated by the ellipse extended along the y -axis (Fig. 3B). This is consistent with slope suspension feeders being represented by multiple TLs feeding on an isotopically similar food source. In contrast, for pelagic feeders, $E_{\text{canyon}} > E_{\text{slope}}$, and positive θ values for the canyon consumers indicated that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are positively correlated. Negative θ values

Table 3. Isotopic niche area ($\%$) estimates (sample size-corrected standard ellipse area, SEA_c ; and Bayesian SEA, SEA_B), including 95 % credible intervals (CI), SEA_c overlap ($\%$), and parameters (eccentricity, E and the angle between the semi-major axis of the SEA_c and the x -axis, θ) calculated from the isotopic values for different feeding groups found in Baltimore Canyon and slope environments. 'Benthic*' combines the benthic, infauna, deposit, epifaunal, and suprabenthic groups. **Bold** values were significantly higher ($p \leq 0.05$)

	N	SEA_c	SEA_c overlap	θ	E	SEA_B	95 % CI
Benthic							
Canyon	30	5.62	4.11	84.63	0.93	5.15	3.76 to 7.63
Slope	181	5.84		-89.50	0.93	5.78	4.97 to 6.70
Benthic*							
Canyon	94	7.43	5.30	86.92	0.88	7.27	5.99 to 8.93
Slope	376	6.14		88.29	0.92	6.10	5.53 to 6.75
Deposit							
Canyon	7	30.07	6.31	-86.86	0.80	23.00	8.53 to 54.24
Slope	21	6.71		62.40	0.98	7.24	4.52 to 11.43
Epibenthic							
Canyon	13	0.41	<0.01	-7.20	0.79	0.35	0.21 to 0.65
Slope	9	3.92		82.51	0.93	3.26	1.52 to 6.77
Infauna							
Canyon	5	5.59	2.55	81.82	0.92	3.81	1.11 to 10.64
Slope	66	5.89		84.51	0.96	5.80	4.48 to 7.29
Suprabenthic							
Canyon	39	3.61	1.98	81.53	0.89	3.44	2.47 to 4.78
Slope	99	3.33		-85.20	0.89	3.27	2.69 to 3.99
Pelagic							
Canyon	67	3.80	1.35	78.84	0.96	3.75	2.94 to 4.77
Slope	74	3.58		-82.33	0.85	3.50	2.79 to 4.38
Suspension							
Canyon	115	8.71	0	62.45	0.88	8.66	7.17 to 10.35
Slope	30	4.12		84.40	0.97	3.91	2.70 to 5.70
Unknown							
Canyon	20	1.61	0	82.79	0.96	1.48	0.95 to 2.35
Slope	77	2.91		64.80	0.81	2.84	2.30 to 3.56

for the pelagic and suprabenthic consumers on the slope indicated that as $\delta^{13}\text{C}$ declines, $\delta^{15}\text{N}$ increases, consistent with our OLS results (Fig. S4). For deposit and epibenthic feeders, the opposite pattern was observed, where θ values were negative for canyon consumers and positive for slope fauna. Consumers in the unknown category had E and θ values that were both greater in the canyon than adjacent slope, illustrated by the more elongated ellipse from in the canyon (Fig. 3A) than slope (Fig. 3B).

Model simulation with reduced sample size and taxa number

Reducing the consumer isotope dataset to 40% resulted in large changes in estimates for SEA_c and SEA_b for deposit feeders (canyon), likely because they had the smallest sample size (Table S5). Reducing the dataset to 5 taxa decreased SEA_c and SEA_b substantially for benthic and infaunal feeders on the slope, despite having 41 and 56 ind. group⁻¹, respectively. These analyses indicate that multiple taxa within these feeding groups increased the breadth of the SEA.

Given the sensitivity of the SEA_c and SEA_b to sample size, feeding groups with the lowest number of individuals (deposit feeders, $n = 8$; and infaunal feeders, $n = 5$) were combined with data from benthic, epibenthic, and suprabenthic feeders, and SEA_c and SEA_b were re-calculated. While SEA_c and SEA_b estimates increased for this new benthic category that included more consumers, canyon suspension feeders still had the largest area estimates overall, followed by benthic, pelagic, and unknown feeders (Table 3). For the slope, benthic feeders had the largest ellipses, followed by suspension, pelagic, and unknown feeders. All canyon feeding groups, except for unknowns, had larger SEA_c and SEA_b values compared to slope groups.

DISCUSSION

Community-wide metrics reveal distinct food webs

Stable isotope data from 129 taxa and calculations of community-wide isotope metrics improved our understanding of a submarine canyon and adjacent slope food webs along the Atlantic margin. Overall, the large spread (CR) and diversity of $\delta^{13}\text{C}$ values for consumer groups found in Baltimore Canyon and adjacent open slopes suggest that the isotopic com-

position of POM changes as a function of multiple factors, including temporal variability in productivity, water depth, and spatial location within the canyon and on the adjacent slopes. Additionally, higher trophic diversity may be influenced by enhanced species diversity, particularly the presence of deep-sea corals in Baltimore Canyon, which we discuss in detail below. Isotope results from slope consumers were similar to ranges reported from other deep-sea environments (Iken et al. 2001, Davenport & Bax 2002, Fanelli et al. 2009). While there was some overlap, all community-wide isotope metrics (e.g. NR, CR, CD, NND) were greater in the canyon than on the adjacent slopes, consistent with our primary hypothesis that isotopic compositions differed between canyon and slope environments, with the canyon having higher trophic diversity.

The higher trophic diversity observed within the canyon may be influenced by the depositional dynamics associated with discrete zones of organic enrichment and resuspension, where OM is being rapidly transported through the canyon and accumulates in specific zones. This is strongly related to the interaction of canyon topography and regional hydrography, which creates enhanced turbulence and mixing within this specific canyon system (Gardner 1989b). The isotopic distinctiveness between canyon and slope environments suggests that the primary food source, POM, undergoes different degradation pathways in these areas (e.g. Dell'Anno et al. 2013), and/or may be influenced by seasonal periodicity in the food supply. Chlorophyll *a* (chl *a*) concentrations in the canyon sediment traps peaked in October 2012 and May 2013, corresponding to post-fall and spring surface plankton bloom periods. While the isotope values for this material did not vary substantially from month to month, these 2 time points corresponded to the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the year (F. Mienis pers. obs.). Chl *a*-rich, fresh food delivered to the seafloor may have supplied consumers with isotopically depleted OM within the canyons. Given that all but 19 of the consumers were collected at the same time of year (August 2012) and that isotopes provide a time-integrated record of assimilated diet (Hobson 1993), isotopic differences between canyon and slope environments may be due to discrete differences in the isotopic composition of the POM source that is spatially constrained and influenced by seasonal patterns. However, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the limited sediment trap data available from this study (-22.8 to -22.0 , 4.3 to 5.1 ‰; Fig. 2, Table S3 in the Supplement) were similar to the isotopic composition of sediment OM (-21.7 ± 0.5 ,

5.7 ± 0.3‰), indicating that isotopic composition of deposited POM is fairly consistent over canyon depth and season. The high turbidity and persistent nepheloid layer (Gardner 1989b) within Baltimore Canyon corresponded to the presence of resuspended POM that is isotopically enriched, leading to higher isotopic composition of consumers and discrete isotopic niches within the canyon trophic system and influencing overall food-web structure.

Food-web length (FWL), which quantifies the number of linkages from primary producers to the highest order consumers, influences energy transfer and trophic cascades in ecosystems (Vander Zanden & Fetzer 2007). While few studies have examined FWL in the deep sea, in general, 3 to 5 TLs have been reported from different regions, habitat types, and depth zones (Iken et al. 2001, Polunin et al. 2001, Bergmann et al. 2009, Fanelli et al. 2009). The canyon and slope food webs examined here supported approximately 5 TLs. This study suggests that Baltimore Canyon and slope areas may be at least as trophically diverse as other deep-sea ecosystems studied to date. However, certain corals and sponges from the canyon had low $\delta^{15}\text{N}$ values and a TL of ~1, which is the TL assigned to primary producers. Low $\delta^{15}\text{N}$ values may result from many factors, including symbiotic nitrogen fixation and/or consumption of bacteria by these suspension feeders (Mueller et al. 2013, Middelburg et al. 2015). Therefore, constraining the food web to 1 TEF (3.4‰) could underestimate the trophic diversity of the system. TEFs are unknown for most deep-sea consumers and have primarily been examined for fish (McCutchan et al. 2003, Vanderklift & Ponsard 2003, Hussey et al. 2014). Several papers have questioned the use of 3.4‰ for TEF, but this value represents the best marine-calibrated TEF available (Minagawa & Wada 1984, Fry 1988) from areas close to the study location (Georges Bank; Fry 1988). If we assume a lower TEF, then our estimates for trophic levels will increase, as will the overall food-web length. Deep-sea taxa specific estimates for TEFs will better constrain the TL supported within canyon and slope environments.

In contrast to TL estimates, trophic diversity inferred from CD was higher within the canyon than on the adjacent slope, indicating increased trophic diversity related to higher food resource availability within the canyon. Higher trophic diversity is consistent with greater diversity in food resources available in canyon environments, in contrast to constrained food resource availability and use along the slope due to reliance on passive deposition of OM. Higher habitat complexity present within the canyon can

increase species richness and diversity, attracting species of different TLs (Cartes et al. 2010, De Leo et al. 2010, McClain & Barry 2010, Morris et al. 2013). These taxa exploit canyon resources and habitat complexity, generating more trophic complexity over time, which has been suggested for hydrothermal vent and seep environments (Cordes et al. 2010, Zapata-Hernández et al. 2014). Thus, canyon morphology, the interaction with the hydrography and related depositional setting may influence the food resources available to the benthos, leading to more complex trophic interactions compared to the adjacent slope.

Isotope metrics of feeding groups reveal diversity in food resource use

Comparisons between the slope and canyon isotope results suggest isotopic niche separation by feeding groups (Figs. 2 & 3), with suspension feeders occupying a distinct trophic niche. Suspension feeders had the most diverse stable isotope data (Fig. 3), as illustrated by the high spread in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Particle selection by suspension feeders can influence their isotopic composition (Iken et al. 2001, Bergmann et al. 2009, Jeffreys et al. 2009, Dubois & Colombo 2014), where larger particles are enriched in heavy isotopes relative to the smaller particles (Rau et al. 1990). The spread in the $\delta^{13}\text{C}$ values suggests some spatial variability in their food resource, with canyon suspension feeders depleted in ^{13}C relative to those found on the slope. While depth has been proposed as being more important than location (canyon vs. slope) in driving isotope patterns of consumers (Romero-Romero et al. 2016), conclusions from this previous work were limited by the few data available from non-canyon environments. In contrast, results from our OLS analysis indicated that both location and depth help drive suspension feeder isotopic compositions, and potentially, niche separation (Fig. S5).

Further comparisons between suspension-feeding anemones and corals indicated that they occupy 2 distinct isotopic niches. Corals had larger SEA_B and SEA_C values than anemones, suggesting corals have greater niche breadth and potentially utilize a higher diversity of food resources. Deep-sea corals have been shown to rely on fresh POM and zooplankton (Kiriakoulakis et al. 2005, Duineveld et al. 2007, 2012). Polyp size, for example, may play a role in food capture ability, influencing coral's functional niche (Quattrini et al. 2017). Given that several corals (e.g. *Lo-*

phelia pertusa, *Anthothela grandiflora*, *Desmophylum dianthus*) had $\delta^{15}\text{N}$ values similar to trap and sediment POM, rather than being enriched by 3.4‰ due to trophic fractionation (Post 2002), there may be some unmeasured component of suspended OM that was not captured here. For example, the OM captured in the traps about 2 m above bottom represents a combination of vertical flux and resuspended material, and analytically separating these 2 sources was not possible here. In contrast, anemones may feed on older and isotopically-enriched OM (Mincks et al. 2008). *Actinoscyphia* sp., *Halcurias* sp., and unknown Actiniaria anemones were collected from within the resuspension zone of the canyon (276 to 523 m), where OM material is likely reworked and degraded, or removed. Additionally, *Actinoscyphia* sp. exhibit biochemical responses to seasonal changes in quality of phytodetritus (Jeffreys et al. 2009), suggesting certain suspension feeders may adapt their feeding strategy when food is limited. The stable isotope results reported here were based on bulk analysis, which averages the isotopic composition of all the biochemical components of an organism's diet (Peterson & Fry 1987). Follow-up compound-specific SIA will help resolve whether the dominant organic matter pools assimilated by anemones are distinct from coral food resources, and will improve understanding of organic resources utilized by canyon and slope consumers in general.

Stable isotope results for benthic feeders also indicated isotopic niche separation (i.e. specialization) among taxa. The higher isotope values of benthic versus suspension feeders in the canyon environment are consistent with consumption of older, more refractory, isotopically enriched OM. The same pattern was observed in the slope benthic and suspension feeders; however, there was greater isotopic overlap with these 2 groups (Fig. 3). Removal of isotopically light lipids in POM during transport to the seafloor (or at the seafloor) and subsequent consumption by benthic feeders helps explain the enrichment of ^{13}C (Mintenbeck et al. 2007) observed in this group (both in the canyon and slope environments). Feeding group assignments were based on the best available information, which is often limited and not species-specific. Certain organisms might switch feeding modes depending on food resource availability, which influences individual-level isotopic composition. However, by examining community-wide metrics across taxa and feeding groups, the pattern of niche separation among feeding groups (benthic, suspension, pelagic, and unknown) was clear.

In conclusion, this study represents the first quantitative comparison of the trophic structure in one canyon and the adjacent open slope environments using both stable isotopes and community-wide metrics. SIA and isotope niches revealed high trophic diversity and distinct niches in canyon versus slope food webs based on analysis of many different taxa and feeding groups, which may be associated with availability of various food resources and habitat complexity. Canyon morphology, habitat heterogeneity, and depositional dynamics may play a role in diversifying associated food webs and niche specialization identified for suspension feeders. By applying trophic niche theory to Baltimore Canyon food webs, this study provides a starting point from which to test whether observed patterns are broadly generalizable to multiple canyon environments or if they are more site-specific and a function of canyon morphology.

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