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Submarine canyons influence macrofaunal diversity and density patterns in the deep-sea benthos

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1 Abstract

Submarine canyons are often morphologically complex features in the deep sea contributing to habitat heterogeneity. In addition, they act as major conduits of organic matter from the shallow productive shelf to the food deprived deep-sea, promoting gradients in food resources and areas of sediment resuspension and deposition. This study focuses on the Baltimore and Norfolk canyons, in the western North Atlantic Ocean, and investigates how different biogeochemical drivers influence canyon and slope macrofaunal communities. Replicated sediment cores were collected along the main axes (~180-1200 m) of Baltimore and Norfolk canyons and at comparable depths on the adjacent slopes. Cores were sorted, assessing whole community macrofaunal (>300 μm) abundance, diversity and standing stocks. Canyon communities were significantly different from slope communities in terms of diversity, abundance patterns and community assemblages, which were attributed to high levels of organic matter enrichment within canyons. There was a significant departure from the expected density-depth relationship in both canyons, driven by enhanced abundances between 800-900 m canyon depths, which was characterised as a deposition zone for organic matter. Bathymetric zonation, sediment dynamics, organic enrichment, and disturbance events were clear factors that structured the benthic communities in both Baltimore and Norfolk canyons. Coupling family-level community data, with sediment grain-size and biogeochemistry data explained community dynamics across depth and biogeochemical gradients, providing further evidence that canyons disrupt macrofaunal diversity and density patterns in the deep-sea benthos.

2 Introduction

Many deep-sea organisms are resource limited by the availability of surface-derived or advected organic material (Billett et al., 1983; Rex et al., 2006; Rowe et al., 1982; Smith et al., 2008), with benthic faunal densities generally declining with increasing depth and distance from the shore (Houston & Haedrich, 1984; Rex et al., 2006; Rowe et al., 1982). In addition, diversity also generally peaks at mid-slope depths (approximately 1500-3000 m) before declining with greater depth (Etter & Grassle, 1992; Rex, 1981; Rex & Etter, 2010). However, this pattern does not appear to be universal (Rex et al., 1997; Stuart et al., 2003). Where differing patterns occur in other basins, they have been attributed to varied environmental conditions (Cosson-Sarradin et al., 1998). Diversity patterns can be disrupted by several factors that act across different spatial and temporal scales (Levin et al., 2001), with the most significant being habitat heterogeneity (e.g., Levin et al., 2010 and references therein), productivity and biological interactions (Rex 1976; 1981). Variation in species diversity is also associated with large-scale variation in sediment grain-size diversity, nutrient input, and productivity as well as oxygen availability, hydrological conditions, and catastrophic events (Levin et al., 2001).

Submarine canyons are often a major source of topographic heterogeneity along continental margins (e.g., Puig et al., 2014) and are often described as biodiversity hotspots in the deep ocean (Levin & Sibuet 2012). Canyons disrupt expected bathymetric patterns in species' diversity, abundance and benthic productivity, largely through the provision of substrate heterogeneity (e.g. Levin et al., 2010), alteration to sediment characteristics (Etter & Grassle, 1992), and elevated organic matter provision (Amaro et al., 2015; De Leo et al., 2010; Martín et al., 2011). Canyons connect the relatively shallow productive shelf to deep-ocean basins, and can act as conduits for the rapid transport of (organic) matter (Harris & Whiteway, 2011). The accumulation of organic material within some canyons appears to substantially enhance organismal abundance and biomass when compared to adjacent areas (e.g. De Leo et al., 2010; Vetter & Dayton 1998). However, due to their complex and often abrupt topography, canyons also give rise to unique physical environments (Puig et al., 2014), even within neighbouring canyons that have similar hydrographic characteristics such as shared water masses and tidally-driven bottom currents (CSA et al., 2017, Prouty et al., 2017). As such, this can lead to some canyons maintaining locally distinct fauna in terms of biomass, abundance and diversity (e.g. Cunha et al., 2011; De Leo et al., 2014; Gunton et al., 2015; Ramirez-Llodra et al., 2010), as

well as high levels of variability at different locations within individual canyons (Cunha et al., 2011; Cúrdia et al., 2004; Gage, 1997; Gunton et al., 2015; Rowe & Menzel, 1971).

The Mid-Atlantic Bight (MAB) on the east coast of the U.S. is known for its high organic inputs, derived from the interplay of the Gulf Stream, and enhanced surface-productivity to the neighbouring shelf and slope (O'Reilly & Busch, 1984). As a result, some deep-sea continental slope and canyon habitats within this region contain high macrofaunal abundances and biomasses (Blake & Grassle, 1994; Blake & Hilbig, 1994; Grassle & Maciolek, 1992, Rowe et al., 1982). Macrofauna data from submarine canyons in this region are scarce, since most of the past research has focused on the continental shelf and slope (Biscaye et al., 1994; Biscaye & Anderson, 1994; Walsh et al., 1988). The MAB contains 13 major canyons, varying in shape, size and complexity (Obelcz et al., 2014). Two of the most studied in this region are Baltimore and Norfolk canyons; these were chosen for the present study, due to potential oil exploration in their vicinity and potential occurrence of exposed hard substrates supporting coral and sponge communities (Brooke et al., 2017; Hecker et al., 1980; 1983; Quattrini et al., 2015).

Over recent decades, the community structure of benthic macro-invertebrates has been used as a tool for monitoring ecosystem health (Borja & Muxika, 2005; Munari & Mistri, 2008) and for identifying biodiversity hotspots, such as canyons (e.g., De Leo et al., 2010). Benthic macro-invertebrates respond rapidly to both anthropogenic and natural disturbance (Pearson & Rosenberg, 1978), making this component of fauna an ideal model to better understand how communities respond to change (Jörgensen et al., 2005; Rice, 2000). One easily interpreted method for detecting change in benthic communities is the comparative assessment of *k*-dominance curves (Clarke et al., 2006; Rice, 2000). Community rank abundance distributions extract universal features (e.g. the species abundance or biomass) of community structure, which are not explicitly a function of the specific taxa present but may be related to levels of environmental disturbance or biological stress across gradients. The method has been applied in the detection of community shifts due to environmental disturbance and stressors, particularly organic enrichment or pollution (Warwick et al., 1990; Warwick & Clarke, 1994; 1998), but more recently in assessing fishery impacts (Yemane et al., 2005) and detecting disturbance in deep-sea habitats (Cunha et al., 2011).

Most studies usually focus on single canyons, often utilising only a few sampling stations to characterise biodiversity and/or physical processes. In this study, using a replicated sampling design across four sampling depths, we present the most detailed assessment to date of the

invertebrate macrofauna and physical processes within two neighbouring canyons and their adjacent slopes. Physical observations from the two canyons imply that there are significant differences in current speeds, organic matter deposition and turbidity regimes, but they are influenced by similar water masses (i.e. similar temperature and salinity gradients; CSA et al., 2017). We suggest that these local-scale and canyon-specific differences will override the larger scale oceanographic drivers of species distributions, leading to distinct community patterns in abundance and diversity between neighbouring canyons.

3 Materials and methods

3.1 Study location

Baltimore and Norfolk canyons are two of the largest shelf-incising canyons in the MAB region (Farre et al., 1983). These two neighbouring (137 km apart) canyons are generally similar in size and length. They have similar orientation to the shelf and bends in the canyon thalweg, making them ideal areas for comparative study (Figure 1). Baltimore Canyon lies 125 km southeast of Delaware Bay and Norfolk Canyon is situated 115 km east of Chesapeake Bay. Both canyons have considerable areas of steep-sided wall habitats (Obelcz et al., 2014) colonised by cold-water stony corals and octocorals (Brooke et al., 2017), and communities of anemones and sea pens (Hecker et al., 1983). The canyons also support diverse fish assemblages (Ross et al., 2015). Although high canyon megafauna abundances have been reported, no significant differences between slope and canyon assemblages have been found (Hecker et al., 1983; Quattrini et al., 2015). Physical observations from the two canyons show substantial differences in current speeds, the location and intensity of turbidity layers, and in organic matter deposition. However, these neighbouring canyons share larger scale hydrography, giving rise to similar temperature and salinity regimes (CSA et al., 2017). For example, Baltimore Canyon demonstrates mean current speeds of 9.26 cm s^{-1} and 6.6 cm s^{-1} at 1082 m and 1318 m, respectively, whilst Norfolk Canyon had higher speeds of 17.6 cm s^{-1} and 9.0 cm s^{-1} at 917 m and 1364 m, respectively (CSA et al., 2017). Baltimore Canyon contains a temporally elevated turbidity zone, forming a layer that extends from 200-600 m and sometimes down to 800 m, largely driven by tidal currents focused by the canyon axis in winter, early spring and sometimes other periods of the year (Gardner, 1989; Prouty et al., 2017). Norfolk Canyon, whilst less studied, demonstrated smaller clouds of suspended sediments that were present at multiple depths in the canyon (CSA et al., 2017). The adjacent slopes of the two canyons appeared to be largely free of these sediment clouds, although some detached turbid layers have been observed moving away from the adjacent mid-slopes near Baltimore Canyon (Gardner, 1989).

3.2 Sampling design

Samples of sediment for macrofauna analysis were collected at Baltimore Canyon, (NOAA ship *Nancy Foster*) in August 2012 (Table 1), followed by sampling in Norfolk Canyon collected in May 2013 (NOAA ship *Ronald H. Brown*). The sampling campaign followed a replicated design along two transects from the shelf break (~200 m) to the continental rise (~1200 m); one tracing the thalweg of the canyon and the other in similar depths along the adjacent slope (Figure 1b and 1c). Four sampling depths were chosen along each transect. Replicate box cores were taken using a 30 cm Ø (0.07 m^2) NIOZ box corer, equipped with a trip valve to prevent flushing of the sample during ascent. Three replicates within each of the four depth intervals (12 samples from each canyon and 12 samples from each adjacent slope) were used for macrofauna community analysis (Table 1).

3.3 Sample processing

Recovered box cores were quality controlled by assessing the level of disturbance on the sediment surface to ensure the intact vertical distribution of sediment layers. Box cores allocated to macrofaunal analysis were processed by the following methods. 1) A polycarbonate push-core (6.35 cm Ø) was inserted into the top 15 cm sediment depth to assess the vertical depth distribution of macrofauna. These sub-cores were sectioned into 0-2, 2-5, and 5-10 cm layers by extrusion and preserved in a 10 % buffered formalin solution (Bourque et al., 2020). 2) An additional push core (6.35 cm Ø) was taken for isotopic analyses (see Demopoulos et al., 2017), and thus was subtracted from total box core surface area and macrofauna density calculations in the present study. 3) Overlying water from the box core was drained over a 300 μm mesh and added to the sample during washing. 4) The top 15 cm of sediment within the box core was removed for whole macrofauna community analysis. The sample was resuspended in filtered (0.2 μm) surface seawater in a 20 L bucket and washed over a sieve of 300 μm mesh size using a gentle shower hose to avoid damage of macrofauna. Samples were preserved and stored in 10 % buffered formalin solution.

The box core allocated for sedimentological analysis was processed as follows: 1) Full length box core sub-cores for sediment grain-size analysis were collected by insertion of a PVC liner (20 cm Ø) to the base of the core, capped and stored at ambient temperature. 2) Smaller acrylic sub-cores (6 cm Ø) were taken for biogeochemical analyses (i.e. organic carbon, nitrogen, stable isotopes and chlorophyll *a*), sliced into 1 cm sections and fractions stored at -20 °C.

3.4 Laboratory analysis

Macrofauna samples were stained with Rose Bengal prior to rinsing over a 300 µm sieve using freshwater under a fume hood. Macrofauna were sorted from the sediment, enumerated using stereo-microscopy and identified to the lowest practical taxonomic unit, most commonly family level (not possible for all taxa), aided by compound-microscopy where required. Overall, 91 taxonomic resources were used in the whole community identifications (See SM Table 1). In certain cases, particularly for some genera of Polychaeta, additional histological stains (Methylene-blue and Methyl green) were used to aid identification. Following sorting, specimens were stored in 70 % Industrial Methylated Spirits. Family level wet weights were determined by blotting excess preservative fluids and weighing using a Satorius Secura analytical balance accurate to 0.0001 g. Tube-dwelling genera were removed from their tubes prior to weighing, although in the case of very small or fragile species (e.g. Oweniidae) this was not always practical or possible. For analysis, biomass and individual weight data were standardised to preserved wet weight (g Wwt m^{-2}) and individual preserved wet weight (g $ind.^{-1}$ m^{-2}) per unit area per taxa.

All samples for sedimentological and biogeochemical analysis were freeze dried and weighed. Grain-size measurements (0-10 cm) were undertaken (bulk fraction) using a Beckman Coulter LS 12 320 particle size analyser that used laser and optical diffraction to determine the particle size (range from 0-2000 µm). Biogeochemistry sediment slices from the cores were analysed for stable carbon (^{13}C) and nitrogen (^{15}N) isotopes, percent organic carbon and nitrogen, and ^{210}Pb in the top 5 cm, and for phytopigments in the surface slice (0-1 cm) using High-Performance Liquid Chromatography and Mass Spectrometry. For a detailed description of the sedimentology methods, see CSA et al. (2017). Intact chlorophyll *a* concentration derived from the phytopigment analysis were taken as a proxy for fresh phytodetrital biomass.

3.5 Data analysis

Univariate and multivariate statistics were performed using PRIMER (PRIMER_E Ltd) statistical software version 6.0 with the PERMANOVA+ add-on (Anderson et al., 2008).

3.5.1 Abundance and biodiversity metrics

Macrofauna diversity was examined using family-level species richness, diversity based on rarefaction analysis for a sample of 100 individuals (ES_{100}; Hulbert, 1971), and Pielou's evenness (*J'*) based on untransformed abundance data using the DIVERSE routine (Clarke & Gorley, 2006). Data were square-root transformed and used to generate Bray-Curtis similarity resemblance matrices. Differences in mean species richness, macrofaunal density (ind. m^{-2}), biomass (g Wwt m^{-2}), individual weight (g $ind.^{-1}$ m^{-2}) and evenness (Pielou's *J'*) were assessed using a three-way crossed univariate and distance-based PERMANOVA (PERmutational Multivariate ANalysis Of Variance; McArdle & Anderson, 2001) and pairwise comparisons performed. The 3-factor model used the following *a priori* defined factors: habitat (Canyon vs Slope, *ha*), site (Baltimore vs Norfolk, *si*), and depth levels 1-4 (1: 180-190 m, 2: 550-555m, 3: 800-900 m, 4: 1110-1180 m, *de*). Because PERMANOVA is sensitive to differences in multivariate dispersion among groups, the PERMDISP routine was used to test for homogeneity of dispersion when significant factor effects were found (Anderson et al., 2008). Where univariate variables failed homogeneity of variance tests (PERMDISP $p < 0.05$) a weighted dispersion transformation (Clarke et al., 2006) was performed, followed if necessary, by removal of extreme outliers (after nMDS visual inspection). Even after transformation, diversity (ES_{100}) did not meet the homogeneity of dispersion assumptions of PERMANOVA and should be noted when interpreting these results. An outlier within species richness and evenness data was also removed from analysis (Norfolk 800 m; RB-13-060) to obtain homogeneity of dispersions (PERMDISP) after weighted dispersion transformation.

3.5.2 Community assemblages

Macrofauna community structure was assessed by examining the overall proportion (% density m^2) of higher-level taxa, i.e. Polychaeta, Oligochaeta, Crustacea, Mollusca, and Other taxa. Other taxa included Anthozoa, Hydrozoa, Sipuncula, Priapulida, Nemertea, Halacaridae, Platyhelminthes, Holothuroidea, Ophiuroidea, Enteropneusta and Xenophyophoroidea. Differences in community assemblages were assessed by PERMANOVA, as a function of three *a priori* factors (crossed and fixed levels; as described in section 3.5.1) with PERMDISP tests, using Bray-Curtis similarities of square-root transformed data (density m^2). Pairwise comparisons followed where appropriate. A Similarity of Percentages analysis (SIMPER) was used to identify the taxa most responsible (≥ 30 % total) for discriminating between and within canyon and slope communities across the depth gradient.

3.5.3 Environmental drivers

Prior to analysis of biogeochemical and grain-size parameters, data were assessed for collinearity using Draftsman plots and Spearman's rank correlation matrices. Highly correlated environmental parameters (R^2 > 0.95) were removed and where necessary, data were transformed (*log x*+0.1) and normalised (Anderson et al., 2008). The influence of environmental drivers on canyon and slope macrofaunal communities was then assessed via DISTLM (DISTance-based Linear Model) multiple regression analyses. DISTLM performs nominal tests of each variable's explanatory power on the community assemblage, building a multivariate statistical model for all possible combinations of predictor variables (See SM Table 2 for a summary of environmental variables used in the explanatory model). Models were run selecting Akaike's Information Criterion for small sample sizes (AICc) and the *BEST* model procedure. DISTLM results were visualised in multivariate space using Principal Component Ordination (PCO) plots, which displayed the significant linear regressions for the environmental variables as eigenvectors.

3.5.4 Community disturbance

Disturbance plays an important role in shaping the structure of populations and whole ecosystems. In this study, disturbance is defined as a perturbation of biotic or non-biotic origin, which causes a change in the spatial patterns of fauna inhabiting an ecosystem, in this case relative to the adjacent habitats, across a depth gradient. To investigate the degree of macrofaunal community disturbance, abundance (ind. m^{-2}) and biomass (g Wwt m^{-2}) data, averaged for each depth along canyon and adjacent slope transects were used to generate abundance-biomass comparison (ABC) curves, where ranked species *k*-dominance curves of abundance and biomass are plotted against the percentage cumulative dominance. ABC curves were developed as a method for assessing the status of disturbed populations, without the need for reference to temporal or spatial series of control samples (Warwick & Clarke, 1994). The ABC procedure generates an associated Warwick statistic (*W*-statistic) as a measure of differentiation between two *k*-dominance curves ranging from -1, severely degraded, to 1, pristine habitats (Clarke, 1990). The shape of the curve and *W-statistic* can be interpreted as an indication of benthic community disturbance when comparing similar communities, based on the degree of community shift to higher species dominance with increasing levels of environmental disturbance (Pearson & Rosenberg 1978; Ramirez-Llodra et al., 2010). The associated ABC *W*-statistics were calculated and compared via the same three-way crossed

PERMANOVA tests (*habitat* x *site* x *depth*). The *W*-statistic as a measure of macrofaunal community disturbance was also included in the environmental DISTLM model.

4 Results

4.1 Sedimentological and biogeochemical variability

Sedimentological analysis was limited by the availability of only single sediment replicates per habitat and depth; therefore, we applied a correlative approach. Sediment grain-size was correlated with depth (sand, R^2 = -0.82, p = 0.014; silt & clay R^2 = 0.81, p = 0.014) in all transects (Figure 2a and 2b). Grain-size patterns differed slightly between canyons and adjacent slopes, generally at shallow depths (<550 m), with Baltimore Canyon exhibiting a sharp increase in the proportions of sand at mid-canyon depths (550 m). In contrast, Norfolk Canyon contained a greater proportion of clay and silt at that depth (Figure 2a-b, SM Table 2), suggesting a more complex pattern in the canyons. Organic carbon and nitrogen were positively correlated with the proportion of silt and clay (R^2 = 0.81, p = 0.015, R^2 = 0.77, p = 0.025, respectively). Relative to their respective adjacent slopes, both canyons were generally more enriched in carbon, nitrogen and chlorophyll *a* than their adjacent slopes across the same depth gradient (Figure 2c-e). Norfolk Canyon and slope were the more enriched compared to Baltimore Canyon and slope. In both canyons, chlorophyll *a* peaked at mid canyon depths (550-555 m; Figure 2c), and slopes generally contained less chlorophyll *a*. In contrast, percent carbon and percent nitrogen increased along the depth gradient, with the highest values found at deeper canyon depths (> 555 m, Figure 2d-e); Norfolk Canyon showed decreases at 800-900 m.

4.2 Biodiversity

A total of 40,208 individuals were extracted from a combined seabed sediment surface area of 2.81 m^2 analysed to a depth of 15 cm, representing 162 taxa across both canyon and slope areas (for full list of taxa see SM Table 3). The canyons yielded a greater number of individuals (23,776) and taxa (142) than adjacent slopes (16,442 individuals from 138 taxa) (SM Table 4). Polychaetes were the most diverse taxonomic group (51 total taxa), followed by bivalves (28 total taxa), and amphipods (20 total taxa). Of the total number of taxa recorded, 25 were found exclusively in the canyon and 23 were found exclusively in slope habitats. The majority of canyon-only taxa were bivalves, whereas peracarid crustaceans and gastropod molluscs comprised most of the slope-only taxa. Both study sites and habitats exhibited differences in the occurrence of rare taxa (singleton taxa, represented by a single individual; doubleton taxa, represented by two individuals). Between the two study areas, Baltimore (canyon and slope

combined) had higher percentages of singleton and doubleton taxa (11 % and 8.5 %, respectively) compared to Norfolk (7.9 % and 7.9 %, respectively). Both canyons combined exhibited higher occurrences of singleton taxa (15.2 %) and doubleton taxa (7.9 %) compared to slopes (7.9 % and 7.3 %, respectively). For a summary of various diversity metrics at each station, see SM Table 4.

4.2.1 Species richness

Species richness generally decreased along the depth gradient, with significant differences identified across sites, habitats and depths (pseudo-F=5.6, P=0.0024; Figure 3a; Table 2 *ha* x *si* x *de* terms). However, the three-way interaction (see pairwise tests in SM Table 5) also highlighted a significant increase at 1180 m, indicating a more complex pattern. Canyon versus slope comparisons showed species richness at Baltimore Canyon was significantly lower than the adjacent slope only at 900 m (pseudo-F=4.4, P=0.0098). In contrast, no significant differences were detected between the Norfolk Canyon or its adjacent slope. Baltimore Canyon had the most distinct depth gradient, where 50 % of observations indicated a significant decrease in species richness (180 m x 550 m, t=2.9, P=0.0354; 180 m x 900 m, t=5.2, P=0.0050), followed by a significant increase at the lowest canyon depth (900 m x 1180 m, t=3.0, P=0.0357). The two slope habitats expressed some differences between depths. Baltimore slope followed the canyon decreasing richness trend with depth in 50% of observations, although not significantly at intermediate depth communities (550 and 900 m), ending with lowest community species richness values in deepest slope habitats, in contrast to the canyon. The Norfolk slope followed the same pattern as Baltimore slope, although only the shallowest slope habitats (190 m) were richer than 555 and 1110 m (t=5.2, P=0.0062; t =3.8, P=0.0195 respectively).

4.2.2 Rarefaction curves, diversity and evenness

Univariate PERMANOVA showed that diversity (ES_{100}) between the two sites did not differ. Overall, slopes were more diverse (ES_{100}) than canyons (Pseudo-F=19.57, P= 0.0002, Table 2). Pairwise comparisons identified differences in diversity across sites, habitats and depths. However, within-depth variability also differed among depths (PERMDISP, P= 0.002), indicating an effect of within-depth variability, as well as a location effect. Between canyons, only Baltimore Canyon 550 m and 1180 m depths were more diverse than Norfolk Canyon (Figure 3b, SM Table 2). In Baltimore, the mid-canyon depth (900 m) showed significantly

depressed diversity (t=11.4, P=0.0004), compared to the slope. Norfolk slopes were more diverse in the deeper sites than the canyon; a pattern also observed in the Baltimore slope and canyon at 900 m (Figure 3b, SM Table 4). Family-level rarefaction curves (SM Figure 1) showed that estimated slope diversity appeared to exceed canyon diversity (indicated by the steeper initial curve compared to canyon habitats). Of the two curves for canyons and slopes (SM Figure 1), the slope did not reach an asymptote, suggesting further sampling may be required to fully assess the diversity on the slope. The rarefaction curves also indicated within canyons, that shallow depths (180-190 m) contributed the most to diversity followed by 900 m depth. The 550 m depth had the steepest curve, suggesting diversity was the least described at this depth, despite relatively high diversity and evenness (Figure 3b and 3c). On the slope habitats 180 m and 900 m depths were the greatest contributors to diversity (SM Figure 1c).

Species evenness differed significantly between habitat, sites and depths (pseudo-F=4.3, P=0.01; Figure 3c, Table 2 *ha* x *si* x *de* term), but there were no significant differences between the two canyons or the adjacent slopes (see pairwise tests in SM Table 5). Evenness within Baltimore Canyon was variable, where 900 m was significantly lower than all other depths. The greatest evenness occurred at the 550 m site followed by the deepest depth (SM Table 5). Comparing Baltimore Canyon and slope, evenness was significantly lower in 50 % of observations (180 and 900 m), where diversity was highest at 900 m (slope). Norfolk Canyon, in contrast, showed no significant differences when compared with the adjacent slope.

4.3 Standing stock

4.3.1 Density

Norfolk Canyon and slopes had the greatest mean densities of macrofauna (SM Table 4; 18,758 ± 4,437 and 17,515 ± 2,400 ind. m^{-2}, respectively), compared to Baltimore Canyon and slope (SM Table 4, 13,399 ± 792 and 7,126 ± 1,242 ind. m^{-2}, respectively). Densities significantly decreased with depth (pseudo-F=14.6, P<0.001) on slopes with the highest at the shallow stations (180-190 m; Table 2, SM Table 5 *ha x de* term), while canyons, in contrast, had a bimodal pattern, with the 180-190 m depths having similar densities to the 800-900 m station, both of which were higher than the other depths in the study (Figure 3d). When compared with slopes, canyons' communities significantly decreased in density at 550-555 m, with a significant increase at 800-900 m (Figure 3d, SM Table 5 *ha x de* term). Lower macrofauna densities were generally found both at deeper depths within canyons and slopes (1110-1180

m), with no significant difference between the two habitats. Norfolk Canyon had significantly higher densities at 550 m compared to Baltimore Canyon at the same depth (SM Table 5 *si* x *de* term).

4.3.2 Biomass

Biomass significantly decreased with water depth (pseudo-F=4.0, P=0.008; Table 2 and SM Table 5). The high biomass observed on the slopes of Baltimore (1180 m) and Norfolk (800 m) contrasted against a generally decreasing biomass with depth, and were attributed to the presence of single large-bodied individuals of Sipunculidae (*Sipunculus norvegicus*; Peanut worm, 3.5 g) and Edwardsiidae (*Edwardsia* spp; Burrowing anemone, 10.0 g) (Figure 3e, SM Figure 2). Norfolk Canyon and slope had a mean macrofaunal biomass of 19.2 ± 9.1 and 38.7 ± 23.7 g Wwt m^{-2}, respectively, whereas Baltimore Canyon and slope were lower, 16.2 ± 4.7 and 11.5 ± 5.3 g Wwt m^{-2}, respectively (SM Table 4), but there were no significant differences between canyons, slopes or the Norfolk and Baltimore study areas (Table 2).

4.3.3 Individual weight

Mean individual weight (g $ind.^{-1}$ m^{-2}) revealed significant differences with water depth (pseudo-F=3.5, P=0.012, Table 2, Figure 3f), but not between sites (Norfolk or Baltimore areas) or habitats (canyons or slopes). Significantly larger bodied macrofauna were found at 550-555m compared to 800-900m (SM Table 5) in canyons. Slope habitats in general, were inhabited by larger-sized macrofauna individuals across the whole depth range, with the smallest-bodied macrofauna occurring in the Baltimore Canyon and slope communities at 900 m.

4.4 Community composition

Across the Baltimore study area, the majority of macrofauna were Polychaeta (46 %) followed by Mollusca (31 %) and Crustacea (12 %). The Norfolk area had higher proportions of Polychaeta (67 %) than the Baltimore area followed by Mollusca (16 %) and Crustacea (6 %). The most notable change in community composition was in Baltimore Canyon (900 m) where large proportions of Mollusca (74 %), namely bivalves (Yoldiellinae and Thyasiridae) contributed greatly to differences between canyon and slope habitats. Baltimore Canyon communities showed higher proportions of Mollusca (36 %) across depth groups compared to the slope (27 %). Additionally, Baltimore slope habitats showed higher proportions of

Crustacea and Oligochaeta (17 % and 8 %). Examining the proportions of phyla biomass in canyon communities (SM Figure 2) revealed that upper canyon communities were dominated, in both canyons by Mollusca (specifically Lucinidae, *Lucinoma foliosa*) and Other phyla (*Actiniaria* spp., specifically Edwardsiidae and Ophiuroidea, namely Amphiuridae sp.) despite Polychaeta and Mollusca being most numerous (SM Figure 2). While polychaete abundance decreased with depth in both canyons, polychaete biomass remained constant in Baltimore Canyon. In Norfolk Canyon, polychaete biomass varied with depth, decreasing at 800 m. On the adjacent slopes, polychaete biomass decreased with depth, although slope habitats showed largest biomass contributions from 'Other Phyla' in both instances, driven by the singular occurrences of large-bodied Sipunculidae on the Baltimore slope at 1180 m and Edwardsiidae spp. on the Norfolk slope at 800 m.

The vertical distribution of macrofauna (maximum 10 cm sediment depth) revealed that more than 50 % of macrofauna were located in the uppermost 2 cm in both canyons and slopes (SM Figure 3). Generally, both canyons and slopes exhibited similar vertical distribution patterns; however, the most distinct change was evident in Baltimore Canyon 900 m sediment where 85% of the macrofauna was located in the upper 0-2 cm of the sediment.

4.5 Community structure

Multivariate PERMANOVA analysis revealed that communities differed significantly between habitats, study sites and across the water depth gradient (Table 3 *ha* x *si* x *de* term). Baltimore Canyon communities differed significantly from Norfolk Canyon at each depth (SM Table 6 *ha* x *si* x *de* term). In contrast, the slopes differed only in the upper communities at 180-190 m and 550-555 m, whilst lower slope community structure was similar between areas (Figure 4). Canyon communities were separated from slope assemblages along differing trajectories (Figure 4, indicated by solid and dashed lines), which was most distinct in the Norfolk study site. Baltimore Canyon communities were divided into two groups (Figure 4a), indicating strongly dissimilar community assemblages between the upper (180 m and 550 m) and lower (900 m and 1180 m) canyon. The upper canyon communities (180 m) and mid-canyon (550 m) were the most distinct, whilst lower canyon communities (990-1180 m) were more similar to lower slope communities.

Community similarity across the depth gradient, (between replicates), was higher in Baltimore Canyon than in Norfolk Canyon, ranging from 81-68 % and 59-48 %, respectively. The larger

similarities among replicates within canyon habitats suggest lower habitat heterogeneity and community patchiness in the canyons in contrast to slope habitats, which in general exhibited lower community similarities across the depth gradient (Table 4). In Baltimore, two bivalve families, namely Thyasiridae and Yoldiellinae, dominated the difference in macrofauna community structure between canyon and slope communities, and both families were found in high abundances (7,322 ± 333 and 3,132 ± 157 ind. m^{-2} respectively) at Baltimore Canyon 900 m (SM Figure 2a). Similarly, Yoldiellinae ranked as third most important taxon separating Norfolk Canyon and slope communities, preceded firstly by Capitellidae and Cirratulidae. Examinations of the taxa contributing to community differences suggest some depth derived zonation pattern exists in canyon and slope community structure. This was most clear in Baltimore Canyon, where taxa driving the macrofauna assemblage turn-over with increasing depth (180-1180 m) were the bivalve families Lucinidae, Yoldiellinae and Thyasiridae, and the polychaete family Spionidae. In Norfolk Canyon, the 800 m assemblages were distinguished from the other canyon communities by two taxa occurring in high mean abundances, namely the polychaete family Capitellidae (12,812 ± 5,188 ind. m^{-2}) and the bivalve Yoldiellinae (2,329 ± 662 ind. m^{-2}), meaning that the two canyons can be differentiated from lower slope assemblages by these four highly dominant taxa. The canyon communities were 59 % dissimilar to slope communities (Table 4b), and the most important discriminating taxa were Dentaliidae, Capitellidae, Ophiuroidea and Nephtyidae, all of which occurred more abundantly in canyons. Slope communities were less dissimilar (52 %) and distinguished by a high contribution from the polychaete taxa Cirratulidae, followed by Oligochaeta and Lumbrineridae.

4.6 Environmental drivers of community structure

DISTLM analysis revealed sediment organic enrichment, grain-size, disturbance and depth all had significant effects on the observed community patterns across both sites and habitats (Tables 5a and 6a). Depth explained the most variation in community assemblages for both the Baltimore and Norfolk areas (17.9 and 20.8 % respectively) followed by the proportion of sand (17.7 % and 20.0 % respectively). In the Baltimore site, $\delta^{15}N$ alone explained 17.2 % of the community pattern followed by the percentages of carbon (11.8 %) and chlorophyll *a* (11.3 %). For the Norfolk study site, stronger relationships were evident, with percent carbon explaining 18.2 % of variation, followed by percent nitrogen (18 %) and chlorophyll *a* (14.4 %). At both sites, community disturbance (*W*-Statistic) explained 11.7 % and 10.4 % of variation in

Baltimore and Norfolk, respectively. The most explanatory multivariate linear regression was for the Baltimore site, which explained 78 % of variation (Table 5b; Chl *a*, % C, % N, $\delta^{13}C$, $\delta^{15}N$, Sand, Depth). In contrast, the most explanatory model for Norfolk, explained 45 % of variation (Table 6b; % N, $\delta^{13}C$, Sand). However, the AICc of the other 9 top models were within 1 unit of the top model, suggesting they are also likely models. Both sites showed strong relationships between macrofauna community structure and depth, sediment grain-size and sediment organic enrichment (Figure 4).

4.7 Community disturbance

Community disturbance analyses (assessed by ABC curves and the *W*-Statistic) revealed considerable species dominance within macrofauna assemblages that were consistent across both study sites (Figure 5). Disturbance was detected in the deeper reaches of the canyons (800-1180 m), as well as in uppermost and mid-slope communities (180-555m) (Figure 5, highlighted by orange and red circles). PERMANOVA results on the community disturbance measure (*W*-Statistic) suggested significant differences in the level of disturbance between canyons and slopes, and depth (Table 2). Pairwise tests revealed increased disturbance occurred within the canyons between mid-canyon (550-555m) and lower canyon depths (1110-1180 m), while for slope habitats community disturbance was significantly higher in the upper shelf break and decreased with depth (SM Table 5 *ha x de* term).

5 Discussion

Several studies have examined the macrofaunal abundance and diversity along the U.S. East Coast continental margin and rise (Blake & Grassle, 1994; Blake & Hilbig, 1994; Hilbig & Blake, 1991; Hecker, 1990; Maciolek et al., 1987). However, only few have focused on macrofauna within canyons, and the present study represents one of the most detailed comparisons of two neighbouring canyon systems with their respective adjacent slopes (Cunha et al., 2011; De Leo et al., 2014; Paterson et al., 2011; Vetter & Dayton, 1998) and is the most detailed for the North American east coast. Using a multi-disciplinary approach that utilised a replicated depth-stratified sampling design, we observed significant differences between the two canyon and slope assemblages, which were structured by strong depth, sediment grain-size and organic enrichment gradients.

5.1 Diversity and productivity in canyons and on slopes

Diversity-depth (i.e. species richness) relationships are generally unimodal, reflecting the well-known macroecological relationship between diversity and productivity across large scales (Kadmon & Benjamini, 2006; Leduc et al., 2012; McClain et al., 2009; McClain & Schlacher, 2015). Typically, in the north western Atlantic, diversity is lower in upper bathyal depths (200-~1000 m) than the lower bathyal zone (~2000 m) followed by a decrease towards the abyss (Etter & Grassle, 1992; Levin et al., 2001; Rex et al., 1997; Sanders, 1968). Our fine-scale study crossing a depth range from 180 m to 1180 m demonstrated more complex patterns and deviation from this expected relationship, both within the canyons and their adjacent slopes. The Baltimore slope demonstrated generally decreasing species richness, but increased diversity with depth, likely due to the linear increase in proportion of finer sediments with depth and consistent organic enrichment. In contrast, the Norfolk slope was more enriched, and bimodal in sediment grain size, giving rise to a less predictable pattern.

A significant departure from the diversity-depth unimodal curve was exhibited in the two canyons, which was attributed to depressed diversity at 900 m depths in Baltimore Canyon. This corresponded with shifts in sediment composition to fine silts and clays and increased sediment organic enrichment, resulting in a concave as opposed to the usual convex unimodal curve. Norfolk Canyon, in contrast, exhibited a less consistent pattern, with suppressed diversity at 800 m. This study represents a relatively small-scale example given the limited depth range sampled, but substantial shifts in diversity patterns were observed due to localised

canyon disturbances. Theoretically, a higher incidence of disturbance shifts the peak of the diversity-depth curve towards higher levels of productivity (Kondoh, 2001; Worm et al., 2002). In this case, supressed diversity at 800-900 m shifted the diversity minimum of the diversity-depth curve to the right, as organic enrichment increased in the canyons. Although there is widespread acceptance of the diversity-depth model in deep-sea ecology, the underlying driving mechanisms remain uncertain (Rex & Etter, 2010). Our study demonstrates that the topographic heterogeneity of the deep sea, coupled with the distinct physical processes that arise, exerts substantial, but not consistent influence on local community patterns (Levin et al., 2010).

5.2 Macrofauna density in canyons and on slopes

The pattern of benthos standing stock density with water depth in the western North Atlantic is well-established, whereby biomass and abundance show an exponential decline from the shelf-break to abyssal depths (Figure 6; Rex & Etter, 2010). Whilst few canyon-specific studies exist for the western North Atlantic, earlier continental margin studies provide some general context for comparisons with the present study (Blake et al., 1985; 1987; Blake & Grassle, 1994; Blake & Hilbig, 1994; Maciolek et al., 1987). Most studies have reported considerable variation in macrofaunal densities on the shelf, especially between shelf break depths and the continental slope (500-1200 m). Slope densities in the present study were within the range previously reported for the continental margin off the northeast USA (Blake et al., 1985; 1987; Blake & Grassle, 1994; Blake & Hilbig, 1994; Houston & Haedrich, 1984; Maciolek et al., 1987).

In contrast, canyon densities were higher than estimates for the more northerly MAB, Hudson Canyon (1,880-9,280 ind. m^{-2}, Rowe et al., 1982) and were more than several times higher than reports for eastern North Atlantic canyons on the Portuguese margin (474-583 ind. m^{-2}, Cunha et al., 2011) and the Whittard Canyon, south of Ireland (2744-6249 ind. m^{-2}, Gunton et al., 2015). In part, our higher densities may result from our analysis of a smaller size fraction (> 300 µm) than Cunha et al. (2011), who analysed the > 500 µm fraction at comparable depths and being shallower than Gunton et al. (~3500 m, 2015). In this study, slope macrofauna density decreased steadily with depth, a typical global pattern for upper continental slopes (Figure 6) (Levin & Gooday, 2003; Rex & Etter, 2010). However, canyon densities were depressed at 550-555 m followed by a sharp rise at 800-900 m, forming a distinct bimodal

density distribution along the canyon axis (Figure 6), driven by the accumulation of organic matter in the lower canyons.

5.3 Biomass and body size in canyons and on slopes

Whilst canyons have been shown to maintain enhanced biomass compared to the slope habitats, e.g. for canyon mega-benthic invertebrates (De Leo et al., 2010), macrofauna communities (Cunha et al., 2011; Escobar-Briones et al., 2008; Vetter & Dayton, 1998) and meiofauna (Ingels et al., 2009; Ramalho et al., 2014), in the present study biomass in the canyons did not differ significantly from the adjacent slope. Biomass estimates were within the range of previously reported estimates from the western North Atlantic continental margin (1.2-12.2 g Wwt m^{-2}, Rowe et al., 1974) and Hudson Canyon (10.4- 46.2 g Wwt m^{-2}, Rowe et al., 1982), although biomass from upper canyon depths (180-190 m) were lower (30.28 g Wwt m^{-2}) than reported for similar depths in Hudson Canyon (46.2 g Wwt m^{-2}, Rowe et al., 1982). In this study, canyon areas that were organically enriched contained macrofauna that had smaller body sizes than slope habitats, reflecting communities dominated by small opportunistic species (Pearson & Rosenberg, 1978). Body size overall, decreased with depth, in agreement with current views (Rex et al., 2006; Wei et al., 2010).

5.4 Macrofauna communities

Shifts in community composition (beta diversity) were evident across the depth gradient, reflecting the bathymetric preferences and niche partitioning of macrofaunal communities (Carney, 2005). For example, Lucinidae (*Lucinoma foliosa*) in the upper canyons and slopes were restricted to upper shelf depths, while Thyasiridae and Yoldiellinae were most common in deeper slope habitats (< 200 m and >500 m, respectively, Oliver et al., 2016). Both sites were numerically dominated by polychaetes, followed by bivalves and crustaceans, with the exception of the bimodal peak in Baltimore Canyon, which exhibited an increase in bivalves. Key community members driving differences between the canyons and slopes were two dominant sub-surface detritivore bivalve families, Thyasiridae and Yoldiellinae. Thyasirid bivalves are burrowing species that favour organic-rich silts and clays (Duperron et al., 2013) and are known to contain chemoautotrophic endosymbionts (Dando, 1991; Dando et al., 1994). Yoldiellinae are also often associated with organically-enriched fine-grained sediments (Grassle & Morse-Porteous, 1987; Quiroga et al., 2012; Reed et al., 2014). In addition, two deposit-feeding opportunistic polychaete families distinguished canyon communities

(particularly in Norfolk Canyon) from other slope habitats, namely Capitellidae and Cirratulidae. Both are well established indicators of disturbance and organic input (Pearson & Rosenberg, 1978) and may indicate different levels of physical disturbance between the two canyon systems.

5.5 Influence of environmental factors on community patterns

There were clear differences in environmental conditions at the two canyons and slopes, suggesting the presence of canyon-specific environmental drivers. The sediment grain-sizes across canyons and slopes generally decreased with increasing depth, as expected for continental margin deep-sea habitats (Gardner et al., 1996; Karl, 2006; Valentine et al., 1980). However, at depths of 550 m in Baltimore Canyon and 800 m in Norfolk Canyon, there were higher proportions of sand, indicative of sediment winnowing (Bouma, 1965; Vetter & Dayton, 1998). Such variation in the distribution of sediments is known to influence organic content and may enable resource partitioning promoting higher faunal diversity (Levin et al., 2001).

Organic matter availability generally decreases with increasing distance from coastal regions. In areas where organic carbon is enhanced through biotic and abiotic factors, elevated standing stocks are common. Submarine canyons are prime examples of this, as topography, bottom currents (Gardner, 1989; Palanques et al., 2006a), upwelling (Allen & Hickey, 2010) and deposition of particulate organic matter (de Stigter et al., 2011; Martín et al., 2006) are important mechanisms that concentrate organic matter in canyons (Cunha et al., 2011; Cúrdia et al., 2004; de Stigter et al., 2007; Kiriakoulakis et al., 2011; Vetter & Dayton, 1998). This study found enrichment to be variable along the canyon depth gradient, to be higher within canyons than adjacent slopes and that Norfolk Canyon was most enriched, by almost two-fold, when compared to Baltimore. Whilst such differences may be a direct consequence of the different timing of sampling (August for Baltimore sampling and May for Norfolk), they demonstrate the spatially and temporally variable nature of these systems even amongst neighbouring canyons and that the high surface productivity of the MAB region can lead to the deposition of significant food supplies (DeMaster et al., 1994; Rex & Etter 2010; Schaff et al., 1992) that concentrate within the canyons.

Combining abundance and biomass data allowed for holistic community assessments of species dominance and standing stock (Clarke, 1990) and confirmed that disruption to the macrofauna community occurred in deeper canyon habitats. These communities were

dominated by burrowing bivalve species Yoldiellinae and Thyasiridae as well as high abundances of Capitellidae, Cossuridae and Gymnonereidinae. The organically-enriched sediments found in the lower canyons likely benefited small-bodied opportunistic species and suppressed diversity and community evenness, a classic benthic response to enrichment processes (Diaz & Rosenberg, 1995; Gray et al., 2002; Pearson & Rosenberg, 1978). However, turbidity flows within canyons are commonplace, and may be an additional stressor that can disturb benthic communities leading to similar responses (e.g. Puig et al., 2014).

Lower community disturbance was detected in the shallower parts of the two canyons (180-555 m), corresponding with enhanced species richness, diversity, community evenness and suppressed densities recorded. Paterson et al. (2011) noted similar occurrences in polychaete assemblages from Portuguese canyons operating under the Dynamic Equilibrium Model (Huston, 1979; Kadmon & Benjamini, 2006), which predicted that when the effects of productivity and disturbance are in balance, diversity will be highest. This may offer an explanation for high diversity and low densities at 550-555 m communities in canyons. In contrast to canyon habitats, the adjacent slopes displayed opposing patterns, whereby upper slopes contained communities that were more disturbed than those deeper. Given the low organic enrichment compared to canyon habitats, this suggests that disturbance at upper slope is likely due to different stressors. A speculative explanation for higher disturbance at shallow slope sites may be associated with impacts from fishing pressure, or the interaction of the shelf with hydrography such as the shelf-break front (CSA et al., 2017). Similar patterns in macrobenthos have been related to trawling activities in other areas (Palanques et al., 2006b; Tuck et al., 1998; Wilson et al., 2015; Yemane et al., 2005).

6 Conclusions

Results of this study support long-held hypotheses about canyons, including their importance as hotspots of biodiversity, and support the argument that sedimentary processes play an important role in forming ecological patterns within the confines of canyon systems (Levin et al., 2001). The results confirm our initial hypothesis that MAB canyons contain distinct macrofaunal communities, which display abundance, diversity and community composition patterns that are different from adjacent slopes. However, biomass and average body size were not conclusively shown to be enhanced in the canyons at all depths. Sediment grain-sizes and organic matter data confirmed the secondary hypothesis that canyon macrofauna communities are structured by strong environmental gradients related to depth, sediment type, and organic enrichment and disturbance regimes, but the relative ranking of drivers varied between the canyons. This suggests that canyon sediment dynamics, biogeochemical gradients and oceanographic regimes act in synergy to create canyon-specific conditions that structure the observed macrofaunal patterns. Differing disturbance patterns were observed between canyons and slopes, supporting the third hypothesis, whereby slopes were more disturbed in shallower areas (< 600 m), and canyons more disturbed in deeper areas (> 800 m). Expected patterns of species richness, diversity and evenness with depth held only in slope habitats, and not within the two studied canyons. The results of this study are congruent with previous studies on macrofauna within submarine canyons worldwide and highlight the important role of canyon habitats in contributing to regional diversity and organic matter cycling on continental margins.

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Tables and Figure captions

Table 1. Locations of stations (decimal degrees) for samples collected in (a) Baltimore Canyon, (b) Baltimore Slope, (c) Norfolk Canyon and (d) Norfolk Slope. * = Box core reserved for geological / biogeochemical assessment in Baltimore. In Norfolk, a sub-core was taken for these variables out of the macrofauna box core due to logistical constraints.

(a)

Baltimore Canyon

Date	Station	Depth (m)	Latitude	Longitude
19/08/12	NF-2012-019	189	38.243217	-73.8436
19/08/12	NF-2012-020*	189	38.243183	-73.84353
20/08/12	NF-2012-028	191	38.242817	-73.84352
20/08/12	NF-2012-029	191	38.242833	-73.84352
20/08/12	NF-2012-030	563	38.1661	-73.85018
21/08/12	NF-2012-032	563	38.166183	-73.85018
21/08/12	NF-2012-034	565	38.166217	-73.85007
21/08/12	NF-2012-035*	567	38.166267	-73.84998
22/08/12	NF-2012-046*	844	38.11722	-73.83532
22/08/12	NF-2012-045	840	38.11722	-73.8358
22/08/12	NF-2012-047	848	38.1174	-73.8348
23/08/12	NF-2012-049	844	38.11752	-73.83453
23/08/12	NF-2012-053*	1120	38.0709	-73.7783
23/08/12	NF-2012-055	1179	38.0724	-73.7732
23/08/12	NF-2012-056	1179	38.0724	-73.7732
24/08/12	NF-2012-062	1180	38.0721	-73.77337

(b)

Baltimore Slope

Date	Station	Depth (m)	Latitude	Longitude
24/08/12	NF-2012-064	168	38.06258	-73.86562
24/08/12	NF-2012-065*	170	38.06258	-73.86558
25/08/12	NF-2012-066	170	38.06258	-73.86562
25/08/12	NF-2012-067	168	38.06258	-73.86562
25/08/12	NF-2012-070*	515	38.04352	-73.80347
25/08/12	NF-2012-072	514	38.04352	-73.80344
25/08/12	NF-2012-076	510	38.04352	-73.80344
26/08/12	NF-2012-088	502	38.0436	-73.8032
26/08/12	NF-2012-082	990	38.01388	-73.7535
26/08/12	NF-2012-084*	990	38.013883	-73.7534
26/08/12	NF-2012-085	991	38.0139	-73.7534
26/08/12	NF-2012-087	991	38.0139	-73.7534
27/08/12	NF-2012-090	1185	37.9774	-73.6694
27/08/12	NF-2012-091*	1185	37.997383	-73.66938
27/08/12	NF-2012-092	1187	37.97742	-73.6694
27/08/12	NF-2012-093	1186	37.97742	-73.6694

Table 1 cont…

(c)

Norfolk Canyon

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-046*	195	37.09475	-74.74658
11/05/13	RB-2013-047	195	37.09478	-74.74657
11/05/13	RB-2013-048	195	37.09478	-74.74657
11/05/13	RB-2013-043*	559	37.07597	-74.66063
11/05/13	RB-2013-044	557	37.07597	-74.66058
11/05/13	RB-2013-045	558	37.07595	-74.66058
10/05/13	RB-2013-040*	805	37.04273	-74.62917
10/05/13	RB-2013-041	803	37.04275	-74.6292
10/05/13	RB-2013-042	804	37.0428	-74.62925
10/05/13	RB-2013-038*	1110	37.03863	-74.57986
10/05/13	RB-2013-039	1110	37.03868	-74.57995
15/05/13	RB-2013-077*	1108	37.03875	-74.57964

(d)

Norfolk Slope

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-049*	187	37.02307	-74.64577
11/05/13	RB-2013-050	187	37.02445	-74.64729
11/05/13	RB-20 13-051	187	37.02415	-74.64594
12/05/13	RB-2013-054*	549	37.0158	-74.5782
12/05/13	RB-2013-055	549	37.0158	-74.57815
12/05/13	RB-2013-056	548	37.0158	-74.57817
13/05/13	RB-2013-059	790	37.00903	-74.56478
12/05/13	RB-2013-060	790	37.00905	-74.56472
14/05/13	RB-2013-069*	804	37.00902	-74.56496
14/05/13	RB-2013-071*	1118	37.00577	-74.53373
15/05/13	RB-2013-073	1105	37.00577	-74.5337
15/05/13	RB-2013-075	1103	37.00588	-74.53365

Table 2. Univariate PERMANOVA 3-factor models analysing patterns in observed diversity (ES_{100}), species richness (Taxa), evenness (Pielou's *J'*), macrofauna density, biomass, individual weight, and community disturbance (*W*-statistic) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), † = square–root or * = weighted dispersion transformed, ‡= significant PERMDISP test (<0.05).

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Diversity (ES_{100}) * ‡						
Habitat (*ha*)	1	1185.4	1185.4	19.571	**0.0002**	9917
Site (*si*)	1	130.89	130.89	2.161	0.1487	9924
Depth (*de*)	3	1357.3	452.43	7.4694	**0.0002**	9955
ha x *si*	1	10.669	10.669	0.1761	0.7164	9924
ha x *de*	3	36.939	12.313	0.2032	0.9186	9940
si x *de*	3	1287.1	427.36	7.0554	**0.0006**	9952
ha x *si* x *de*	3	732.36	244.12	4.0303	**0.0132**	9947
Residual	32	1938.3	60.571			
Total	47	6673.9				
Species richness (Taxa) *						
Habitat (*ha*)	1	24.426	24.426	0.31857	0.6075	9924
Site (*si*)	1	126.89	126.89	1.655	0.2021	9935
Depth (*de*)	3	1405.7	468.56	6.1112	**0.0023**	9954
ha x *si*	1	10.027	10.027	0.13077	0.7860	9934
ha x *de*	3	145.04	48.347	0.63057	0.6129	9945
si x *de*	3	121.37	40.456	0.52765	0.6861	9956
ha x *si* x *de*	3	1277.4	425.8	5.5535	**0.0024**	9948
Residual	32	2376.8	76.672			
Total	47	5418.5				
Evenness (*J'*) *						
Habitat (*ha*)	1	0.08977	0.08977	0.04073	0.8484	9890
Site (*si*)	1	4.7935	4.7935	2.1747	0.1468	9877
Depth (*de*)	3	7.5676	2.5225	1.1444	0.3541	9956
ha x *si*	1	1.9594	1.9594	0.88893	0.3533	9890
ha x *de*	3	23.789	7.9297	3.5976	**0.0226**	9952
si x *de*	3	5.4328	1.8109	0.82158	0.4935	9955
ha x *si* x *de*	3	28.618	9.5394	4.3278	**0.0098**	9957
Residual	31	68.33	2.2042			
Total	46	145.32	0.08977			

Table 2 cont…

Factor	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
Macrofauna density (ind. m^{-2}) †						
Habitat (*ha*)	1	700.9	700.9	4.7774	**0.0228**	9934
Site (*si*)	1	1,393.5	1,393.5	9.498	**0.0017**	9937
Depth (*de*)	3	6,432.1	2,144	14.614	**0.0001**	9944
ha x *si*	1	311.88	311.88	2.1258	0.1351	9946
ha x *de*	3	3,190.6	1,063.5	7.2493	**0.0002**	9950
si x *de*	3	1,216.4	405.48	2.7638	**0.0321**	9942
ha x *si* x *de*	3	456.8	152.27	1.0379	0.3935	9953
Residual	32	4,694.8	146.71			
Total	47	18,397				
Biomass (g Wwt m^{-2}) †						
Habitat (*ha*)	1	467.29	467.29	0.86238	0.3834	9941
Site (*si*)	1	343.08	343.08	0.63314	0.4857	9944
Depth (*de*)	3	6,473.7	2,157.9	3.9823	**0.0077**	9954
ha x *si*	1	517.94	517.94	0.95584	0.3521	9945
ha x *de*	3	1571	523.68	0.96644	0.4348	9934
si x *de*	3	838.64	279.55	0.5159	0.7642	9947
ha x *si* x *de*	3	824.6	274.87	0.50726	0.7617	9951
Residual	32	17,340	541.87			
Total	47	28,376				
Individual weight (g ind.$^{-1}$ m^{-2}) †						
Habitat (ha)	1	351.23	351.23	0.59318	0.5148	9939
Site (*si*)	1	152.45	152.45	0.25746	0.7382	9937
Depth (*de*)	3	6130.9	2043.6	3.4514	**0.0118**	9963
ha x *si*	1	107.11	107.11	0.1809	0.8198	9950
ha x *de*	3	3355.6	1118.5	1.889	0.1149	9963
si x *de*	3	2374.7	791.56	1.3368	0.2663	9945
ha x *si* x *de*	3	1377.3	459.09	0.77533	0.5680	9944
Res	32	18948	592.12			
Total	47	32797				
Community disturbance (*W*-Statistic) †						
Habitat (*ha*)	1	3.1142	3.1142	0.98962	0.3271	9895
Site (*si*)	1	24.5	24.5	7.7855	**0.0101**	9910
Depth (*de*)	3	98.096	32.699	10.391	**0.0001**	9965
ha x *si*	1	0.01182	0.01182	0.00376	0.9787	9913
ha x *de*	3	121.12	40.375	12.83	**0.0002**	9958
si x *de*	3	16.695	5.5651	1.7685	0.1734	9948
ha x *si* x *de*	3	4.1157	1.3719	0.43596	0.7336	9959
Res	32	100.7	3.1469			
Total	47	368.36				

Table 3. Multivariate PERMANOVA 3-factor model analysing patterns in observed macrofauna community structure (square–root transformed) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), after transformation all factors met the assumptions of the permutations of dispersions test (PERMDISP $p > 0.05$).

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Habitat (*ha*)	1	5,325.9	5,325.9	9.0651	**0.0001**	9916
Site (*si*)	1	5,601	5,601	9.5333	**0.0001**	9920
Depth (*de*)	3	18,971	6,323.7	10.763	**0.0001**	9910
ha x *si*	1	3,807.3	3,807.3	6.4804	**0.0001**	9910
ha x *de*	3	8,148.9	2,716.3	4.6234	**0.0001**	9870
si x *de*	3	6,187	2,062.3	3.5102	**0.0001**	9859
ha x *si* x *de*	3	8,438.7	2,812.9	4.7878	**0.0001**	9864
Residual	32	18,801	587.52			
Total	47	75,280				

Table 4. Similarity Percentage (SIMPER) analysis for macrofauna assemblages at canyon and adjacent slope habitats, showing (sub)families or higher taxa (Total ≥ 30 %) contributing the most to (a) average similarity differences within canyon and slope depth groups, and (b) average dissimilarity between canyon and slope habitat.

(a)

Baltimore Canyon (75.0 %)							
180 m (81.6 %)		**550 m (66.6 %)**		**900 m (81.4 %)**		**1180 m (68.9 %)**	
Lucinidae	8.0	Spionidae	9.5	Yoldiellinae	18.9	Thyasiridae	6.0
Cossuridae	7.6	Cirratulidae	7.8	Thyasiridae	12.3	Capitellidae	5.6
Dorvilleidae	5.1	Oligochaeta	6.9			Gymnonereidinae	5.4
Oweniidae	5.0	Polycirrinae	6.0			Nemertea	5.2
Paraonidae	4.3					Aplacophora	5.1
						Cossuridae	4.7
Baltimore Slope (65.6 %)							
180 m (69.0 %)		**550 m (58.8 %)**		**900 m (67.4 %)**		**1180 m (67.1 %)**	
Paraonidae	14.2	Thyasiridae	11.2	Oligochaeta	7.6	Macrostylidae	8.0
Oligochaeta	7.5	Paraonidae	11.9	Macrostylidae	5.9	Aplacophora	6.9
Cirratulidae	6.4	Nuculidae	8.1	Paraonidae	5.6	Paraonidae	6.8
Onuphidae	4.8			Aplacophora	5.1	Oligochaeta	6.1
				Maldanidae	4.9	Tanaidomorpha	5.8
				Tanaidomorpha	4.5		
Norfolk Canyon (63.3 %)							
190 m (58.7 %)		**555 m (68.2 %)**		**800 m (58.1 %)**		**1110 m (68.4 %)**	
Cossuridae	12.8	Oligochaeta	9.4	Capitellidae	20.2	Yoldiellinae	10.1
Paraonidae	8.7	Dentaliidae	8.6	Yoldiellinae	10.1	Dentaliidae	8.8
Ophiuroidea	6.7	Capitellidae	7.0			Cossuridae	8.1
Oligochaeta	5.4	Maldanidae	6.7				
Norfolk Slope (65.5 %)							
190 m (78.0 %)		**555 m (73.9 %)**		**800 m (48.6 %)**		**1110 m (61.6 %)**	
Paraonidae	11.9	Cirratulidae	18.7	Thyasiridae	13.8	Thyasiridae	8.2
Oligochaeta	6.6	Paraonidae	9.9	Paraonidae	13.0	Gymnonereidinae	6.3
Ampharetidae	6.5	Lumbrineridae	6.9	Phoxocephalidae	12.2	Cirratulidae	5.4
Cirratulidae	5.7					Maldanidae	5.0
						Lumbrineridae	5.0
						Paraonidae	5.0

Table 4 Cont…

(b)

Baltimore (56.7 %)		**Norfolk (53.7 %)**		**Canyons (59 %)**		**Slopes (52 %)**	
Canyon vs Slope		**Canyon vs Slope**		**Baltimore vs Norfolk**		**Baltimore vs Norfolk**	
Thyasiridae	5.5	Capitellidae	7.6	Dentaliidae	6.5	Cirratulidae	15.5
Yoldiellinae	4.9	Cirratulidae	5.7	Capitellidae	5.6	Oligochaeta	5.1
Cossuridae	4.4	Yoldiellinae	4.0	Ophiuroidea	4.8	Lumbrineridae	4.1
Paraonidae	2.7	Cossuridae	3.5	Nephtyidae	3.8	Spionidae	3.3
Dentaliidae	2.6	Paraonidae	3.0	Oligochaeta	3.7	Paraonidae	3.2
Nuculidae	2.5	Dentaliidae	2.8	Cossuridae	3.6		
Phoxocephalidae	2.4	Ophiuroidea	2.7	Maldanidae	3.5		
Oligochaeta	2.3	Nephtyidae	2.6				
Pelecypoda	2.1						
Maldanidae	1.9						

Table 5. Distance-based linear modelling (DISTLM) on species abundance data at Baltimore Canyon and adjacent slope showing (a) the proportion of macrofaunal assemblage pattern explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	SS (trace)	Pseudo-*F*	P (perm)	Prop. (%)
Depth	6,365.4	4.7891	0.001	17.9
% Sand	6,318.8	4.7465	0.001	17.7
$\delta^{15}N$	6,132.3	4.5772	0.001	17.2
% Carbon	4,201.1	2.9429	0.003	11.8
Chl *a*	4,012.6	2.7941	0.003	11.3
W	4,158.8	2.9094	0.001	11.7
$\delta^{13}C$	3,856.7	2.6724	0.003	10.8
% Nitrogen	3,328.7	2.2688	0.017	9.3

(b)

AICc	R^2	RSS	Selections
164.2	0.78291	7,729.9	Chl *a*, % C, % N, $\delta^{13}C$, $\delta^{15}N$, Sand, Depth
167.25	0.70141	10,632	Chl *a*, % N, $\delta^{13}C$, $\delta^{15}N$, Sand, Depth
167.25	0.70135	10,634	Chl *a*, % N, $\delta^{13}C$, $\delta^{15}N$, Depth
167.32	0.70051	10,664	Chl *a*, % N, $\delta^{15}N$, Sand, Depth
167.77	0.63860	12,868	Chl *a*, % C, % N, $\delta^{13}C$, Depth
167.97	0.69228	10,957	*W*, Chl *a*, % C, $\delta^{15}N$, Sand, Depth
168.15	0.79438	7,321.3	*W*, Chl *a*, % C, % N, $\delta^{13}C$, $\delta^{15}N$, Sand, Depth
168.19	0.63212	13,099	Chl *a*, % N, $\delta^{13}C$, Sand, Depth
	Total SS (trace):	35,607	

Table 6. Distance-based linear modelling (DISTLM) on species abundances at Norfolk Canyon and adjacent slope showing (a) the proportion of macrofaunal assemblage pattern explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	SS (trace)	Pseudo-*F*	P (perm)	Prop. (%)
Depth	7,077.7	5.768	0.0001	20.8
% Sand	6,804.8	5.4901	0.0001	20.0
% Carbon	6,196.9	4.8906	0.0001	18.2
% Nitrogen	6,135.1	4.8312	0.0001	18.0
Chl *a*	4,909.1	3.7032	0.0005	14.4
$\delta^{13}C$	4,012.9	2.9369	0.0045	11.8
$\delta^{15}N$	3,777.4	2.7431	0.0076	11.1
W	3,533.4	2.5454	0.0136	10.4

(b)

AICc	R^2	RSS	Selections
170.09	0.44692	18,845	% N, $\delta^{13}C$, Sand
170.15	0.4454	18,897	% C, $\delta^{15}N$, Sand
170.17	0.44491	18,913	% N, $\delta^{15}N$, Sand
170.24	0.58135	14,265	Chl *a*, % C, % N, $\delta^{13}C$, Sand
170.28	0.51268	16,604	Chl *a*, % C % N, $\delta^{13}C$
170.31	0.44171	19,022	% C, $\delta^{13}C$, Sand
170.45	0.50923	16,722	% N, $\delta^{13}C$, $\delta^{15}N$, Sand
170.56	0.43588	19,221	Chl *a*, Sand, Depth
170.66	0.43356	19,300	% N, Sand, Depth
170.68	0.36029	21,797	% N, Sand
	Total SS (trace):	34,073	

Figure 1. Maps of study locations: (a) Study area in the Mid-Atlantic Bight, western North Atlantic showing location of the two canyons, (b) Baltimore Canyon box cores (white circles) collected along canyon and adjacent slope transects in 2012 across comparable depths and (c) Norfolk Canyon and adjacent slopes sampled in 2013. Bathymetry on all figures is shown as the inset colour scale bar.

Figure 2. Sediment parameters for Baltimore and Norfolk canyons (grey squares) and adjacent slopes (white squares) across the depth gradient. (a) Percent sand, (b) percent silt and clay, (c) surface chlorophyll *a*, (d) percent organic carbon and (e) percent organic nitrogen.

Figure 3. Biodiversity and abundance measures (mean ± 1 SE.) for Baltimore and Norfolk canyons (grey bars) and adjacent slope (white bars), across the depth gradient. (a) species richness, (b) diversity (Shannon-Wiener *H'*) and (c) evenness (Pielou's *J'*), (d) macrofauna density, (e) total biomass, (f) individual weight.

Figure 4. Principal Component Ordination for benthic community assemblages, including environmental eigenvectors (blue lines), based on square-root transformed abundance data at (a) Baltimore Canyon and adjacent slope, and (b) Norfolk Canyon and adjacent slope. Environmental parameters included sediment grain-size, surface sediment chlorophyll *a*, percent organic carbon, percent total nitrogen, $\delta^{13}C$, $\delta^{15}N$, *W*-Statistic and depth. Arrows on each plot indicate the general pattern for canyon (solid line) and slope (dashed line), extending from shallow to deep stations.

Figure 5. Abundance (Grey) biomass (Black) comparison (ABC) curves based on mean macrofaunal density (ind. m^2) and biomass (g Wwt m^2) data for Baltimore and Norfolk canyons and adjacent slopes across the depth gradient. Moderately disturbed (orange circles) and severely disturbed (red circles) community structure are highlighted. *W* is the associated Warwick statistic, a measure of distance between the two dominance curves (-1 = very disturbed, 1 = undisturbed).

Figure 6. Density against productivity and enrichment. The dashed lines on both plots refer to the expected pattern (Rex & Etter 2010), which complied to our data for the adjacent slopes (canyon and slope are conceptually drawn as opposed to statistically fitted). The solid line reflects the divergent pattern that was observed in the Baltimore and Norfolk canyons.