

# The role of habitat heterogeneity and canyon processes in structuring sediment macrofaunal communities associated with hard substrate habitats in Norfolk Canyon, USA

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1	Title: The role of habitat heterogeneity and canyon processes in structuring sediment
2	macrofaunal communities associated with hard substrate habitats in Norfolk Canyon, USA
3	
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11	
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13	
14	Abstract
15	Topographic and hydrodynamic complexity in submarine canyons promotes steep
16	gradients in food availability and geophysical parameters which affect ecological assemblages
17	and beta diversity. While habitat heterogeneity in submarine canyons is known to support diverse
18	and abundant megafaunal communities, due to difficulty in sampling little is known about
19	infaunal communities adjacent to hard substrate habitats, their contribution to canyon
20	assemblages, and overall deep-sea diversity. Sediments were collected in three distinct habitat
21	types: within Norfolk Canyon (western Atlantic) adjacent to the canyon walls, along the main
22	axis of the canyon, and on the adjacent continental slope to quantify macrofaunal (>300 $\mu$ m)
23	density, diversity and community composition, and sediment geochemical parameters including

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24 grain size, organic content, and stable isotope composition. While macrofaunal densities were 25 similar among habitats sampled at comparable depths, diversity was higher near the hard 26 substrate environments. Discrete communities were present in each habitat type, while annelid 27 functional composition was similar between adjacent to hard substrate and canyon axis habitats. 28 Although diversity and abundance of hard substrate adjacent sediment communities did not 29 change with depth, communities were driven by sediments with low organic matter content, 30 whereas canyon and slope community assemblages were best explained by depth and higher 31 organic content. Beta diversity among hard substrate adjacent sediments and canyon axis 32 communities was high, with 27% of canyon taxa and 10% of regional taxa only occurring in hard 33 substrate habitats. Given the thousands of submarine canyons worldwide, our results highlight 34 the overall importance of substrate habitat heterogeneity within canyons in supporting deep-sea 35 benthic diversity and suggest that both within-canyon and regional diversity are underestimated. 36 37 **Keywords** 

38 Submarine canyon, macrofauna, community, functional trait, habitat heterogeneity39

#### 40 Introduction

Submarine canyons are morphologically complex features along continental margins,
providing heterogeneous habitats and acting as conduits for the transport of sediment and organic
matter from the productive continental shelves to food-deprived abyssal plains (Puig *et al.*,
2014). Habitat heterogeneity is created by the wide range of environmental conditions provided
by variations in topography, hydrodynamic patterns, and sediment transport processes that
support gradients in food resources and areas of sediment resuspension and deposition (De Leo

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47 et al., 2010; Puig et al., 2014) at both local (Huvenne et al., 2011) and regional scales (De Leo et 48 al., 2014). Sediment transport and accumulation (García et al., 2008) represent important 49 influential ecological drivers. Locally enhanced organic matter concentrations (De Leo et al., 50 2010; Duineveld et al., 2001) combined with substrate heterogeneity (Levin and Sibuet, 2012) 51 potentially explain higher faunal diversity, abundance, and benthic productivity found in canyon 52 systems compared to surrounding areas (Cunha et al., 2011; De Leo et al., 2010; Escobar 53 Briones et al., 2008; Gunton et al., 2015a; Gunton et al., 2015b; Ingels et al., 2009; Robertson et 54 al., 2020). However, the dynamic nature of canyons can result in rapid changes in composition 55 of benthic assemblages on both small (1-100 m) and large (1-10 km) scales (Bernardino et al., 56 2019; Campanyà-Llovet et al., 2018; Gambi et al., 2019; Gunton et al., 2015a; Ingels et al., 57 2009; Ingels et al., 2011; McClain and Barry, 2010), which can make comparisons among areas 58 location dependent.

59 In addition to the soft-sediment habitats that dominate canyon environments, hard 60 substrates often occur in multiple forms, including outcrops of bedrock along canyon walls, as 61 boulders previously deposited by turbidity flows, wall failures, or glaciers and icebergs, and 62 along the upper rims of the canyon. Hard substrates are characterized by exposed rock or 63 consolidated mud with steep slopes with elevated current conditions that minimize sedimentation 64 (Huvenne *et al.*, 2011). The presence of hard substrates increases the habitat heterogeneity 65 present in canyon systems by providing additional niches that can support more complex and 66 diverse biological assemblages (Pierdomenico et al., 2017). Rich and diverse coral and 67 invertebrate communities often colonize canyon hard substrates (Huvenne et al., 2011; Orejas et 68 al., 2009; Quattrini et al., 2015), sustained by suitable current conditions for food delivery, with 69 soft-sediment habitats at their base. The influence of hard substrates can extend to nearby

habitats (e.g. Bourque and Demopoulos, 2018; Demopoulos *et al.*, 2014), with sedimentary areas
adjacent to hard substrates acting as deposition zones and containing high amounts of organic
matter that fall down the steep slopes (McClain and Barry, 2010).

73 Habitat heterogeneity at multiple spatial scales (from 10 m to 10 km) within a system is a 74 major factor in structuring faunal assemblages and promoting higher diversity (Campanyà-Llovet 75 et al., 2018; De Leo et al., 2014; Gambi et al., 2019; McClain and Barry, 2010) by influencing 76 organic matter spatial distribution (Campanyà-Llovet et al., 2018). Hard substrates within 77 submarine canyons have been studied primarily in the context of the presence of cold-water 78 corals (e.g. Baker et al., 2012; Mortensen et al., 2005; Orejas et al., 2009; Quattrini et al., 2015) 79 due to their status as critical and sensitive species and habitats; however, little research has been 80 conducted on the adjacent sediment macrofaunal communities (but see Campanyà-Llovet et al., 81 2018; McClain and Barry, 2010). In the Monterey submarine canyon complex, McClain and 82 Barry (2010) found different patterns in macrofaunal density, diversity, and species richness 83 relative to distance from canyon cliff faces at different locations, with high species turnover 84 occurring within 30 m of the canyon walls. In addition, sediments adjacent to cliff faces had 85 increased mass flux of organic carbon to the sea floor with larger sediment grain size and lower 86 percent organic carbon compared to sediments located farther from the cliff face (McClain and 87 Barry, 2010). Similarly, near-wall sediments in Barkley Canyon had a higher mean grain size 88 and lower organic carbon content than similar depths within the main canyon axis (Campanyà-89 Llovet et al., 2018). Further evidence of increased megafaunal activity (e.g. bioturbation) in 90 near-cliff sediments suggests that sediment macrofauna residing adjacent to hard substrates are 91 experiencing high levels of disturbance, resulting in distinct communities (McClain and Barry, 92 2010) that increase the overall biodiversity of submarine canyon systems.

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93	Norfolk Canyon, located in the western north Atlantic Ocean, is a large shelf-incising
94	canyon containing areas of steep-sided wall habitats (Obelcz et al., 2014) colonized by cold-
95	water corals and other invertebrates (Brooke et al., 2017), and large areas of soft-sediments
96	throughout the main axis (Robertson et al., 2020). Norfolk Canyon exhibits relatively high
97	current speeds and suspended sediment clouds are present at multiple depths (200-1200m) along
98	the axis (CSA et al., 2017). Macrofaunal density, diversity, and composition within Norfolk
99	Canyon differed from adjacent slope habitats with sediment dynamics and organic enrichment
100	disrupting generalized depth-related patterns within the canyon and supporting distinct
101	communities at discrete depths (Robertson et al., 2020). In particular, mid-canyon (800 m) and
102	shallow slope (190-550 m) locations were identified as being areas of severely disturbed
103	community structure due to enhanced deposition and erosion/winnowing respectively (Robertson
104	et al., 2020). However, the degree to which different canyon habitats, including hard substrate
105	adjacent sediments, contribute to the overall regional diversity remains unknown.
106	Here we investigate the infaunal community structure and functional composition of
107	sediment communities adjacent to hard substrates in comparison to main-axis habitats within
108	Norfolk Canyon and sediments on the adjacent continental slope by addressing the following
109	questions: 1) are sediment communities adjacent to hard substrates similar to canyon axis and
110	slope soft sediment communities; 2) are any similarities among hard substrate adjacent and
111	canyon axis sediment communities based on geographic proximity or depth regimes; 3) how do
112	sediment communities residing near hard substrates contribute to overall canyon and regional
113	diversity; and 4) what environmental factors drive the community structure and function among
114	hard substrate adjacent and canyon axis sediment communities?

#### 116 Methods

# 117 <u>Sampling Procedures</u>

118 Sediment samples were collected adjacent to hard substrate habitats in Norfolk Canyon in 119 2013 aboard the NOAA Ship Ronald H. Brown (2-18 May 2013) (Figure 1a, Supplemental Table 120 1). Push cores (6.35 cm diameter) were opportunistically collected at 11 individual locations, 121 typically at the base of vertical walls or next to large boulders where soft sediment had 122 accumulated (Fig 1b), during six dives using the ROV Jason II at depths ranging from 400-1342 123 m. At each sampling location 1-2 cores were collected for macrofaunal (>300  $\mu$ m) analysis and 124 one core for sediment geochemical analysis. Additional sediment samples (Figure 1a, 125 Supplemental Table 1) were collected along the main axis of Norfolk Canyon (190 m, 550 m, 126 800 m, 1100 m, 1600 m) and at similar depths on the adjacent continental slope (190 m, 550 m, 127 800 m, 1100 m) using a NIOZ box corer in 2012 (NOAA Ship Nancy Foster, 19-28 Sept 2012, 128 N=6) and 2013 (NOAA Ship Ronald H. Brown, 10-18 May 2013, N=24) with 3-4 replicate box 129 cores per location. Although the inclusion of multiple year samples adds potential seasonal 130 and/or interannual variability to the canyon axis and slope locations, similar analyses as those 131 described below where the 2012 samples were excluded provided similar results and are thus included here to increase replication. Due to lower resolution local bathymetry available at the 132 133 time of sampling, the 190 m slope cores technically occurred within the defined bounds of 134 Norfolk Canyon (see Figure 1a) as later determined by higher resolution bathymetry, but are 135 included as representative slope locations in comparison to the 190m axis cores.

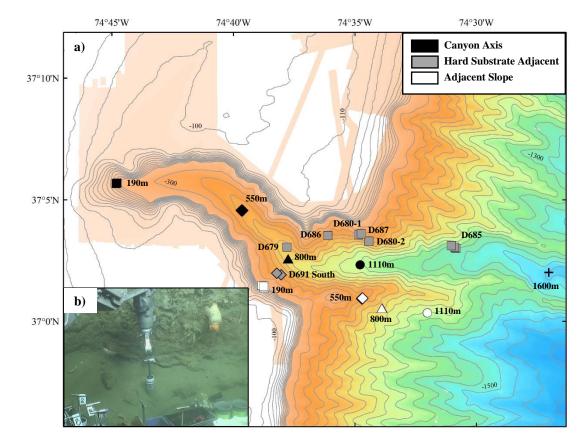


Figure 1. a) Map of sampling locations adjacent to hard substrate habitats (gray), in the main axis
of Norfolk Canyon (black), and on the adjacent slope (white) with depth group or dive location
labels. b) Example of sediment sampling adjacent to hard substrate habitats. Depth contours: 10
m (0-200 m) and 100 m (>200 m).

148 Box cores were subsampled with two polycarbonate push cores (6.35 cm diameter) 149 identical to the ROV-deployed push cores, one each for faunal and sediment chemistry analyses. 150 All push cores were sectioned vertically (0-2, 2-5, 5-10 cm) after recovery for either faunal or 151 sediment geochemical analysis. Vertical distribution of fauna for canyon axis and slope samples 152 was presented in Robertson *et al.* (2020). Faunal core sections were preserved whole in 8% 153 buffered formalin solution until they were washed through a 300-µm mesh sieve to retain the 154 macrofauna portion. Sediment geochemistry core sections were frozen whole in the field at -155 20°C.

156 Macrofauna were sorted with a dissecting microscope and identified to the lowest 157 practical taxonomic level, including family level for polychaetes, oligochaetes, peracarid 158 crustaceans, and molluscs. Homogenized subsamples of geochemistry cores were analyzed for the stable carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) isotopes, and percent organic carbon and nitrogen. 159 160 Grain size analysis was performed on all hard substrate adjacent sediment geochemistry cores 161 and a single replicate of canyon axis and slope cores using the Folk method (Folk, 1968). 162 Station, community, and sediment geochemistry are presented in CSA et al. (2019) and Bourque 163 et al. (2020). Data for the 0-5 cm vertical fractions from the 1600 m canyon axis stations were 164 previously presented in Bourque et al. (2017).

165

166 Data Analysis

167 Macrofaunal Communities

168 Community structure was assessed using multivariate analysis and by examining the 169 overall contribution of individual taxa to the community composition. Multivariate analysis of 170 community structure across all samples was performed on presence/absence transformed data

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171 using Bray-Curtis similarities in PRIMER version 7 (Clarke and Gorley, 2015) with the 172 PERMANOVA+ add on package (Anderson et al., 2008). Cluster analysis (CLUSTER) 173 combined with similarity profile analysis (SIMPROF) was used to determine similarity 174 groupings among hard substrate adjacent sediment communities. Communities were examined 175 using non-metric multidimensional scaling (nMDS) and permutational analysis of variance 176 (PERMANOVA) to test for differences among habitats (hard substrate adjacent, canyon axis, 177 slope) and their respective groupings as follows: CLUSTER-assigned groups for hard substrate 178 adjacent sediments and depth for canyon axis and slope sediments. Similarity of percentages 179 (SIMPER) was used to identify the taxa responsible for discriminating between habitats and 180 groups and to assess the variability of the communities within groups. The RELATE function in 181 Primer 7 was used to test for similarity in community structure with geographic distance within 182 hard substrate adjacent sediment communities and among hard substrate adjacent and canyon 183 axis sediment communities. A resemblance matrix was created with distances between sampling 184 locations to remove the effect of co-located replicates and compared to the Bray-Curtis similarity 185 matrix of community composition. An additional RELATE was performed using the Bray-Curtis 186 similarity matrix of square-root transformed abundance with a Bray-Curtis similarity matrix of 187 presence/absence transformed data to assess the influence of taxa density on the overall 188 similarity results.

189

190 Diversity

Within habitat (alpha) and between habitat (beta) diversity were examined using the total
number of taxa present in each core (Sp), Shannon diversity (H'log<sub>e</sub>), taxa richness estimated
using Marglef's index (d), and Pielou's evenness (J') based on untransformed abundance data

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using DIVERSE in PRIMER Statistical Software version 7 (Clarke and Gorley, 2015). Colonial
organisms (e.g. Porifera and Bryozoa) were excluded from diversity calculations (H', J', and d)
and multivariate community analysis but included in total taxa counts. Beta and regional
(gamma, all habitats) diversity were examined using total taxa counts, shared taxa, and
rarefaction curves calculated using the program EstimateS and plotted for each habitat type and
for all samples combined. A Venn diagram was constructed to visualize the shared and unique
taxa among habitats.

201

202 Univariate analyses

203 Density of macrofauna and univariate measures of biodiversity and sediment 204 geochemistry were analyzed using one-way analysis of variance (ANOVA) with habitat and 205 group as factors and individual cores as replicates, followed by post-hoc test Tukey's HSD for 206 multiple comparisons. All data were tested for normality and heteroscedasticity using Shapiro-207 Wilk and Bartlett's tests (Zar, 1999) and loge-transformed when necessary. If transformation did 208 not achieve normality, a non-parametric Kruskal-Wallis test was used on univariate measures. 209 Sediment geochemical values were averaged across the vertical depth gradient per core prior to 210 analysis. Depth relationships with abundance, diversity, and sediment geochemistry measures 211 were tested using Spearman's rank correlation. A significance level of p < 0.05 was used in all 212 tests. Univariate statistics were computed with the program R (R Development Core Team, 213 2018).

214

215 Functional composition

216 Annelid functional composition was assessed by assignment of individual families into 217 four traits (feeding method, feeding location, motility, and living habit) with 15 total modalities 218 based on published trait information. A trait matrix was created using a 'fuzzy coding' procedure 219 (Chevenet et al., 1994) which allows for flexibility in assigning taxa with a mixture of trait 220 characteristics while capturing potential intraspecific variation in trait expression (Castella and 221 Speight, 1996; Charvet et al., 2000; Chevenet et al., 1994; Demopoulos et al., 2018). A station 222 by trait matrix was created by multiplying taxa abundance by trait values and summing across 223 each core, standardized, and a Bray-Curtis similarity matrix was created. The functional trait-224 weighted community data were analyzed using nMDS and PERMANOVA to test for differences 225 among habitats and groups.

226

# 227 Relationship to environmental drivers

228 To further address the relationship of the environmental variables to the multivariate 229 community and functional composition data, distance-based linear modeling (DistLM) and 230 distance-based redundancy analysis (dbRDA) were performed using the PERMANOVA+ add on 231 package. DistLM performs nominal tests of each variables explanatory power on community 232 structure and builds a multivariate statistical model of explanatory power of a suite of variables 233 when considered together. Community data were averaged for each sampling location due to the 234 single grain size data available for each sampling location. Variables included were depth, mud 235 content, percent organic carbon (%C), percent nitrogen (%N), stable carbon isotope composition  $(\delta^{13}C)$ , stable nitrogen isotope composition ( $\delta^{15}N$ ), and the carbon to nitrogen ratio (C:N). The 236 237 explanatory variables used were not correlated to any other variable included in the model and 238 were chosen due to their potential to structure and/or impact sediment communities.

## 240 **Results**

# 241 Hard substrate adjacent sediment communities

242 Cluster analysis of hard substrate adjacent sediment communities identified two 243 significant community clusters (Figure 2 & 3a, SIMPROF p=0.029), with one group comprised 244 of the sediment communities along the northern canyon wall (North), and the second group 245 comprised of sediment communities along the southern canyon wall (South). North and South 246 clusters had an average similarity of 36.1% (SIMPER), with higher abundances of Yoldiidae 247 (Bivalvia), Scaphopoda, Thyasiridae (Bivalvia) in North samples and higher abundances of 248 Tubificinae (Oligochaeta) and Cossuridae (Polychaeta) in South samples accounting for 26.1% 249 of the dissimilarity. The North cluster had an average similarity of 46.7% (SIMPER) with 250 Paraonidae (Polychaeta), Scaphopoda, Yoldiidae (Bivalvia), Tubificinae (Oligochaeta), and 251 Cossuridae (Polychaeta) accounting for 56.6% of the similarity among samples. In contrast, the 252 South cluster had a lower average similarity of 39.3% (SIMPER) with just two taxa, Paraonidae 253 (Polychaeta) and Tubificinae (Oligochaeta) accounting for 58.4% of the similarity among 254 samples. In comparison to presence/absence transformed similarities, the taxonomic composition 255 had a significant effect on the overall similarity among samples (RELATE  $\rho=0.90$ , p=0.001). 256 The North cluster was characterized by high proportions of Paraonidae (14.6%) and other 257 Polychaeta (17.6%), scaphopods (6.8%), and bivalves (19.2%), but low proportions of

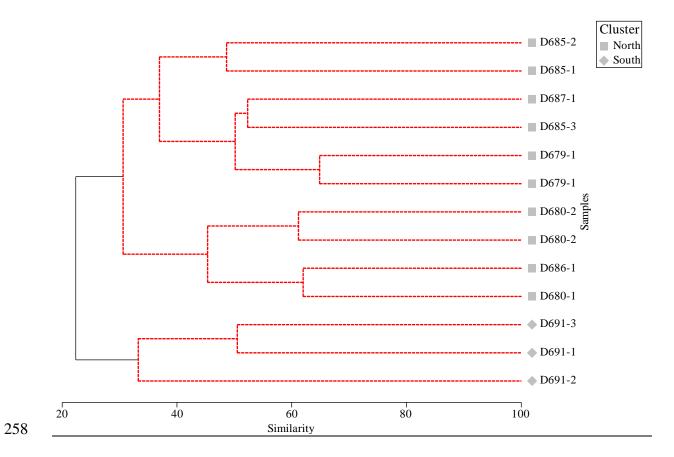
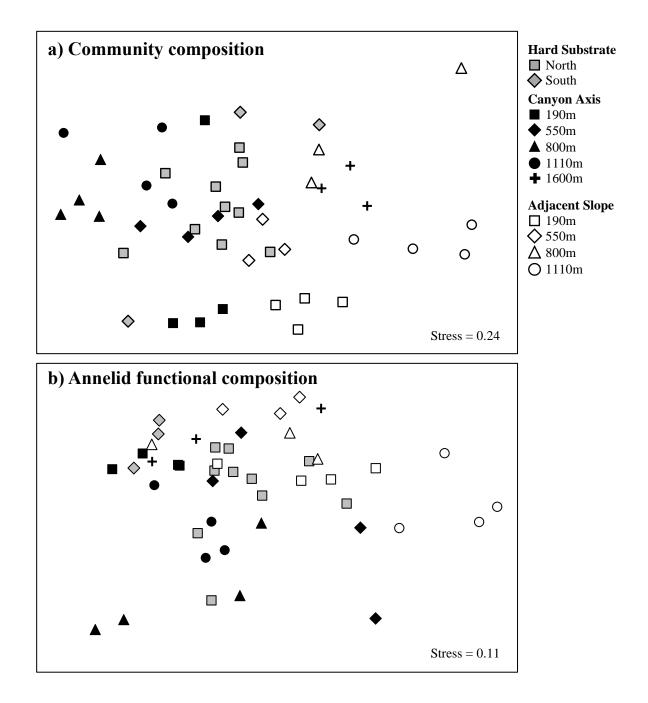


Figure 2. Dendrogram of hard substrate adjacent sediment communities from cluster analysis
using Bray-Curtis similarities of square-root transformed abundance data. Solid black lines
indicate significant differences among groups based on SIMPROF analysis.



270

Figure 3. Non-metric multidimensional scaling of cores collected adjacent to hard substrate habitats (grey symbols), in the canyon axis (black), and on the adjacent slope (white) a) based on Bray-Curtis similarities of square-root transformed abundance data and b) based on Bray-Curtis similarities of standardized annelid functional composition.

oligochaetes (5.0%) (Figure 3). The South cluster was characterized by high proportions of
Cossuridae (22.7%) and Paraonidae (17.5%, Polychaeta) and oligochaetes (27.8%), but lower
proportions of molluscs (2.1%) (Figure 4).

279 Macrofaunal density was similar between the North and South clusters (Table 1, Figure 280 5, ANOVA,  $F_{1-11}=2.89$ , p=0.15) and there was no relationship with depth either across all 281 samples (Spearman correlation,  $\rho=0.121$ , p=0.69) or within the North cluster (Spearman 282 correlation,  $\rho$ =-0.04, p=0.92). The South cluster exhibited a more even vertical density 283 distribution of taxa (Table 1), while the North cluster had the major proportion of taxa in surface 284 sediments. The total number of taxa was much lower in the South cluster (21) than in the North 285 cluster (61); however, the South cluster consisted of only 3 samples while the North cluster was 286 represented by 10. Overall the North and South clusters shared 17 of a total 65 taxa, with only 4 287 taxa unique to the South cluster. Both Shannon diversity (ANOVA,  $F_{1-11}=15.24$ , p=0.011) and 288 species richness (d, ANOVA,  $F_{1-11}=7.92$ , p=0.016) were significantly lower within the South 289 cluster while taxa evenness (J', ANOVA, F<sub>1-11</sub>=1.93, p=0.19) was similar between North and 290 South clusters. Similar to density, there was no correlation with any of the diversity metrics with 291 depth for the North cluster (Spearman correlation: H'loge,  $\rho$ =-0.57, p=0.08; J',  $\rho$ =-0.085, 292 p=0.81; d, p=-0.36, p=0.29).

293

#### 294 <u>Hard substrate adjacent sediment functional composition</u>

Hard substrate adjacent sediment communities were composed primarily of subsurface dwellers (>65%), burrowers (>69%), motile species (>73%), and deposit feeders (>84%) with higher proportions of the above four traits within the South cluster (Figure 6). There was a significant difference in annelid functional composition between the North and South clusters

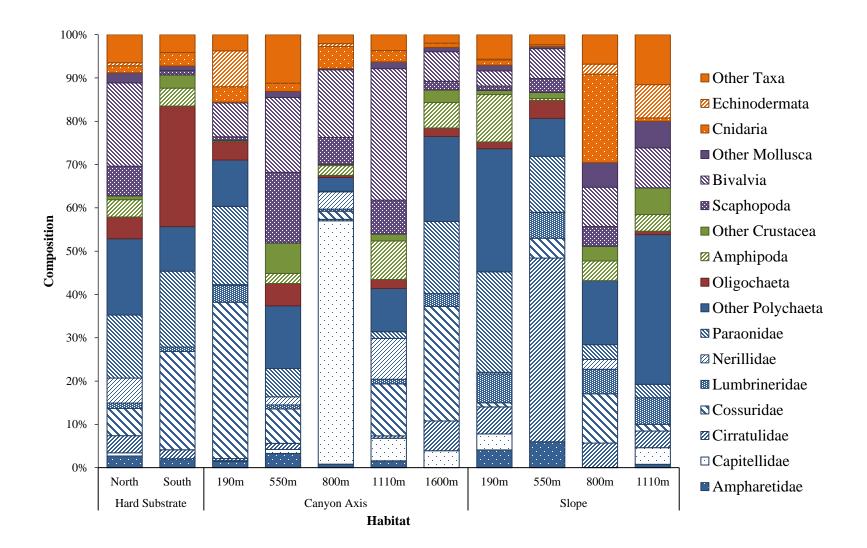


Figure 4. Major taxonomic composition of hard substrate adjacent, canyon axis and slope macrofaunal communities. Color represents
 major taxonomic groups: Polychaeta (blue), Oligochaeta (red), Crustacea (green), Mollusca (purple), all other groups (orange).

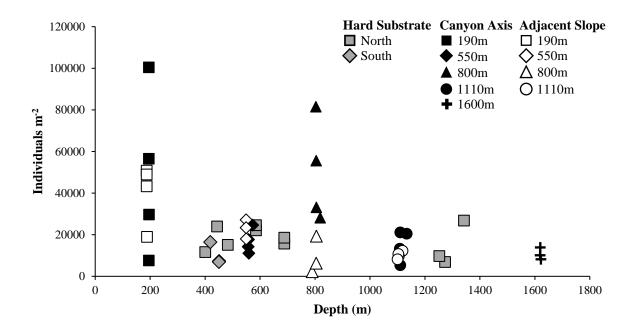


Figure 5. Scaled raw macrofaunal density in hard substrate adjacent, canyon axis, and slopesediments.

- - -

Habitat	Ν	De	nsity	0-2 cm	2-5 cm	5-10cm		d		J'	<b>H'</b> (	log <sub>e</sub> )	Taxa
Hard Substrate	13	15871	(1960)	58.65	25.27	16.08	4.37	(0.40)	0.87	(0.02)	2.46	(0.11)	65
North	10	17567	(2151)	63.67	23.02	13.31	4.86	(0.40)	0.88	(0.02)	2.62	(0.09)	61
South	3	10216	(3108)	29.90	38.14	31.96	2.71	(0.36)	0.83	(0.06)	1.91	(0.17)	21
Canyon Axis	19	29101	(6034)	51.60	34.34	14.06	3.71	(0.22)	0.79	(0.04)	2.18	(0.11)	64
190m	4	48578	(19987)	32.20	47.15	20.65	3.86	(0.64)	0.73	(0.02)	2.10	(0.13)	39
550m	4	16904	(2914)	71.03	18.22	10.75	4.54	(0.33)	0.90	(0.02)	2.62	(0.09)	33
800m	4	49605	(12199)	63.38	29.46	7.17	3.16	(0.48)	0.59	(0.12)	1.67	(0.37)	34
1110m	4	15087	(3701)	59.16	27.23	13.61	3.42	(0.30)	0.87	(0.04)	2.27	(0.12)	30
1600m	3	10742	(1672)	41.18	34.31	24.51	3.65	(0.52)	0.88	(0.06)	2.28	(0.23)	23
Adjacent Slope	14	21395	(4237)	53.06	39.77	7.17	4.90	(0.37)	0.85	(0.03)	2.50	(0.12)	76
190m	4	40521	(7366)	62.18	34.11	3.70	5.86	(0.68)	0.81	(0.03)	2.73	(0.22)	51
550m	3	22854	(2658)	36.41	54.84	8.76	4.06	(0.10)	0.73	(0.03)	2.12	(0.05)	31
800m	3	9268	(5141)	40.91	44.32	14.77	3.91	(1.26)	0.92	(0.04)	2.19	(0.36)	31
1110m	4	10269	(860)	53.08	33.85	13.08	5.32	(0.14)	0.94	(0.00)	2.80	(0.03)	40

Table 1. Mean ( $\pm$  1 S.E.) macrofaunal density and diversity in hard substrate adjacent, canyon axis, and adjacent slope sediments. Density=Individuals m<sup>-2</sup>; d= Margalef's species richness; J'= Pielou's evenness; H'(log<sub>e</sub>)=Shannon diversity; Taxa=Number of taxa. Values in parentheses represent one standard error.



Figure 6. Annelid functional composition a) feeding mode b) feeding location c) motility d)living habit

327

329	(Figure 3b; PERMANOVA, Pseudo-F=5.85, p=0.008) despite a high average similarity between
330	the clusters (SIMPER, 83.7%). Average similarity was high within both the North (87.5%) and
331	South (92.5%) clusters.
332	
333	Comparisons of hard substrate adjacent communities to canyon axis and slope communities
334	Hard substrate adjacent sediment communities differed from both canyon axis
335	(PERMANOVA, t=1.352, p=0.0293) and slope (PERMANOVA, t=1.919, p=0.0001) sediment
336	communities (Figure 3a). Canyon axis and slope communities also differed (PERMANOVA,
337	t=1.97, p=0.0002). Hard substrate adjacent sediment communities were overall more similar to
338	canyon axis communities (SIMPER 38.3%) than to slope communities (SIMPER 32.6%)
339	indicating a general canyon effect. Geographic distance between sampling locations adjacent to
340	hard substrates and the canyon axis was not a significant factor in structuring sediment
341	communities (RELATE, $\rho$ =0.24, p=0.077). The North hard substrate adjacent communities were
342	significantly different from the canyon axis 190 m (p=0.001), 800m (p=0.0006), 1110 m
343	(p=0.01), and 1600 m (p=0.015) communities, while the South hard substrate adjacent
344	communities were only significantly different from the canyon axis 800 m (p=0.011)
345	communities. Differences in taxonomic composition (Figure 4) played an important role in
346	structuring differences among hard substrate adjacent, canyon axis, and slope communities, with
347	a significant correlation between abundance Bray-Curtis similarities and presence/absence Bray-
348	Curtis similarities (RELATE, p=0.88, p=0.001).
349	Macrofaunal densities in hard substrate adjacent sediments were similar to densities
350	observed in the canyon axis sediments at the closest comparable depths (550 & 1110 m, Figure
351	5). Hard substrate adjacent sediments collected at depths <700 m had much lower densities than

352	their geographically closest 800 m canyon axis location, while hard substrate adjacent sediments
353	collected at depths >700 m were similar to their closest geographic canyon axis location at 1600
354	m (Figure 5).
355	
356	Comparisons of hard substrate adjacent communities to canyon axis and slope functional
357	<u>composition</u>
358	While canyon and hard substrate adjacent sediment functional composition did not differ
359	(Figure 3b, PERMANOVA, t=1.15, p=0.27), the functional composition differed between hard
360	substrate adjacent sediments and slope habitats (PERMANOVA, t=2.82, p=0.0034). Canyon
361	functional composition also differed from slope habitats (PERMANOVA, t=3.22, p=0.0004).
362	Slope communities had lower proportions of deposit feeders (50-87%) and higher proportions of
363	omnivores (2-26%), surface feeders (33-57%), motile (44-71%) and sessile (0.8-9.7%) fauna
364	(Figure 6).
365	
366	Within-canyon and regional diversity
367	A total of 653 macrofaunal individuals were collected from sediment cores adjacent to
368	hard substrates. Individuals encompassed 65 taxa, including 31 polychaete families, 9 crustacean
369	families, and 14 molluscan families. An additional 1,750 macrofaunal individuals were collected
370	from the canyon axis and 948 in slope habitats. Slope habitats had 76 taxa encompassing 35
371	polychaete families, 18 crustacean families, and 14 molluscan families, while canyon axis had 64
372	taxa encompassing 30 polychaete families, 10 crustacean families, and 16 molluscan families. A
373	total of 98 taxa were encountered across all three habitats.

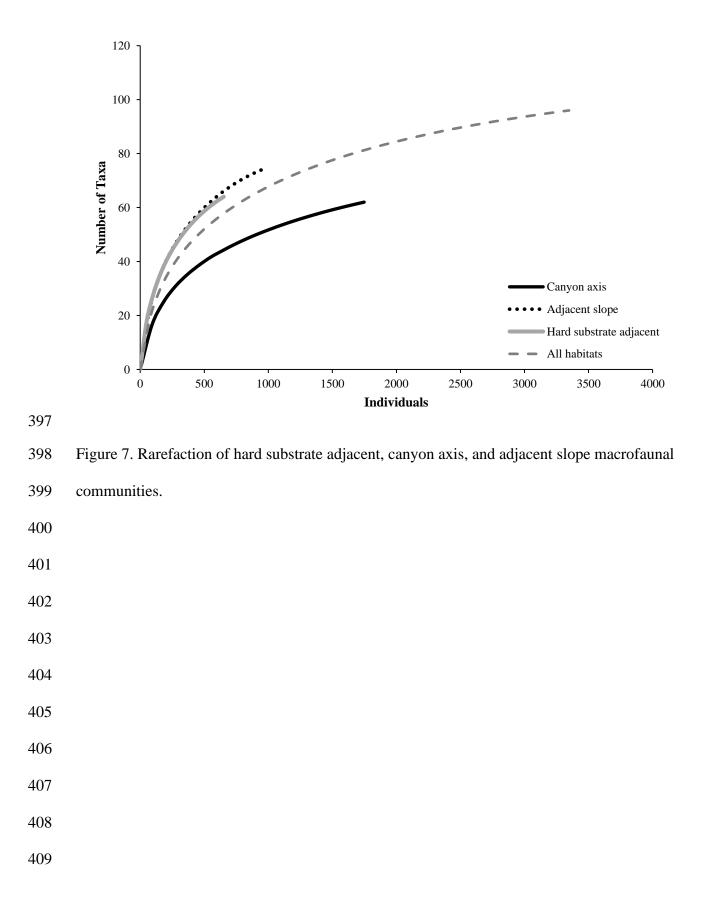
Diversity differed among hard substrate adjacent, canyon axis, and slope communities (Figure 7). Shannon diversity (H') of hard substrate adjacent sediment locations on the north side of the canyon was higher than comparable depths (550 m & 1110 m) in the canyon axis and adjacent slope, while diversity of hard substrate adjacent sediments on the south side of the canyon were similar to those observed at 550 m in the canyon axis (Table 1). Rarefaction of all hard substrate adjacent sediment samples exhibited higher diversity than for all samples collected in the canyon axis across a wider depth range but was similar to the adjacent slope (Figure 7).

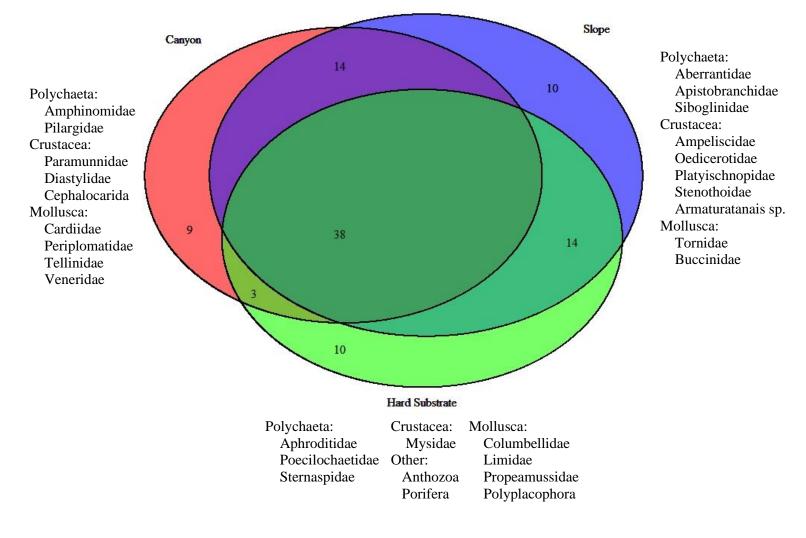
381 There was high beta diversity among hard substrate adjacent sediment habitats, canyon 382 axis, and slope sediments (Figure 8). Canyon axis, slope, and hard substrate adjacent sediment 383 habitats shared 38 taxa (38.8%), while 31 taxa were shared among any two habitats (31.6%) and 384 29 taxa (29.6%) were only found in a single habitat. Of the 29 unique taxa, 9 were found in 385 canyon axis habitats and 10 each in hard substrate adjacent sediment and slope habitats. When 386 considered together, hard substrate adjacent sediments account for 27% of all the taxa 387 encountered within Norfolk canyon and 10% of the taxa encountered within the Norfolk 388 Canyon/slope region as a whole.

389

## 390 Environmental drivers of macrofaunal communities

391 For hard substrate adjacent sediment habitats, only sediment C:N significantly increased 392 with water depth (Spearman correlation,  $\rho=0.656$ , p=0.0.028 correlation). Compared to canyon 393 and slope habitats, hard substrate adjacent sediments had significantly lower percent organic 394 carbon than canyon habitats (p=0.0026), and significantly lower C:N than slope habitats 395 (p=0.0008) (Table 2).





- 410
- 411

412 Figure 8. Beta diversity of hard substrate, canyon axis, and slope habitats. Listed taxa are those exclusive to a single habitat.

414 Table 2. Mean sediment geochemical values for hard substrate adjacent, canyon axis, and slope

Habitat	%	Mud	δ <sup>13</sup>	°C	%	Corg	δ	<sup>15</sup> N	0	ωN	С	:N
Hard Substrate	67.5	(3.5)	-21.1	(0.1)	0.9	(0.1)	6.3	(0.1)	0.2	(0.0)	6.0	(0.4
North	67.7	(4.9)	-21.3	(0.3)	0.8	(0.1)	6.2	(0.1)	0.2	(0.0)	6.1	(0.5
South	66.8	(2.6)	-21.1	(0.2)	0.9	(0.1)	6.5	(0.1)	0.2	(0.0)	5.5	(0.5
Canyon Axis	73.6	(8.8)	-21.2	(0.1)	1.9	(0.2)	6.8	(0.2)	0.3	(0.0)	8.0	(0.5
190 m	42.3	-	-21.4	(0.3)	1.3	(0.4)	6.5	(0.1)	0.2	(0.0)	7.0	(1.6
550 m	63.0	-	-21.1	(0.3)	1.4	(0.3)	7.5	(0.9)	0.2	(0.0)	6.8	(0.1
800 m	46.3	-	-21.0	(0.3)	2.3	(0.2)	6.8	(0.4)	0.3	(0.0)	10.4	(1.4
1110 m	77.4	-	-21.3	(0.2)	2.2	(0.3)	6.6	(0.4)	0.3	(0.0)	8.1	(0.9
1600 m	95.4	(0.4)	-21.2	(0.0)	2.3	(0.2)	6.6	(0.1)	0.4	(0.0)	7.5	(0.8
Adjacent Slope	49.2	(17.2)	-21.6	(0.2)	1.7	(0.4)	5.6	(0.3)	0.2	(0.0)	11.2	(1.4
190 m	20.6	-	-21.9	(0.4)	0.9	(0.4)	5.8	(0.7)	0.1	(0.0)	13.7	(4.6
550 m	18.5	-	-22.1	(0.5)	0.9	(0.3)	5.6	(0.3)	0.1	(0.0)	11.3	(1.0
800 m	77.3	-	-21.2	(0.2)	2.1	(0.7)	5.7	(0.4)	0.2	(0.1)	9.3	(1.1
1110 m	80.5	-	-21.3	(0.3)	2.8	(0.9)	5.4	(0.8)	0.3	(0.1)	10.2	(1.4

415 habitats. Numbers in parentheses indicate the standard error of the mean.

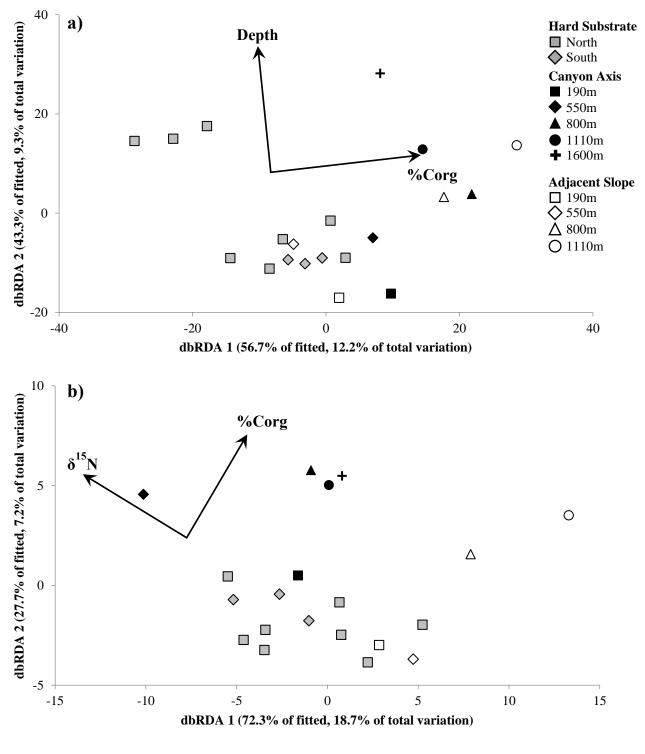
428 DISTLM analysis of macrofaunal communities indicated that four of the seven 429 explanatory environmental variables individually explained a significant portion of the 430 community variation (Table 3). The "best" model identified %Corg explaining 11.6% of the 431 community variation and the second "best" model within 1 AICc identified both %Corg and 432 depth explaining 21.6% of the community variation. Distance-based redundancy analysis (Figure 433 9a) of the "best" two-variable model indicates that hard substrate communities are predominantly 434 separated from canyon and slope communities due to lower %Corg, while depth separates 435 communities within all three habitat types. Seven additional models were within 1 AICc of the 436 top model (Table 3), with 2-variable models that included %Corg combined with either depth (21.5%), percent mud (21.2%), or  $\delta^{13}$ C (20.6%) serving as potential explanatory models. 437 438 Environmental variables structured annelid functional trait composition differently than the macrofaunal communities. Of the seven explanatory variables only  $\delta^{15}N$  composition explained a 439 440 significant portion (16.5%, p=0.036) of the variation in functional composition (Table 4). The "best" model included  $\delta^{15}$ N alone, while the "best" two-variable model (within 1 AICc unit of 441 the top model) included both  $\delta^{15}$ N and %Corg and explained 25.8% of the variation in functional 442 443 trait composition (Table 4). The dbRDA of the two-variable model (Figure 9b) indicates that 444 %Corg separates hard substrate adjacent sediment functional composition from both canyon axis 445 and slope composition, while  $\delta^{15}$ N separates individual locations of hard substrate adjacent 446 habitats and canyon and slope communities.

Variable	SS(trace)	Pseudo-F	Р	Proportion		
and slope environments.						
communities in N	communities in Norfolk Canyon axis, hard substrate adjacent,					
(DISTLM) of environmental variables with macrofaunal						
Table 3. Results from the distance-based linear modeling						

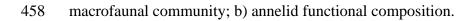
Variable	SS(trace)	Pseudo-F	P	Proportion
$\delta^{13}C$	3033.4	1.796	0.027	0.091
%C	3869.2	2.356	0.001	0.116
$\delta^{15}N$	1685.5	0.956	0.551	0.050
%N	2691.1	1.576	0.078	0.080
C:N	2641.5	1.544	0.076	0.079
% Mud	2901.2	1.711	0.031	0.087
Depth	3131.2	1.860	0.016	0.094

AICc	R <sup>2</sup>	RSS	Selections
150.68	0.11574	29562	%Corg
151.07	0.21585	26215	%Corg, Depth
151.15	0.21247	26328	% Mud, %Corg
151.17	0.093663	30300	Depth
151.23	0.090738	30397	$\delta^{13}C$
151.31	0.20614	26539	$\delta^{13}$ C, %Corg
151.32	0.086781	30530	% Mud
151.46	0.080497	30740	%N
151.49	0.079013	30789	C:N
151.84	0.18504	27245	% Mud, %N
Total SS(trace)		33431	

...\_



457 Figure 9. dbRDA of top two-variable DISTLM model of environmental variables for a)



Variable	SS(trace)	Pseudo-F	P	Proportion
$\delta^{13}C$	123.2	0.832	0.447	0.044
%C	187.4	1.297	0.267	0.067
$\delta^{15}N$	281.6	2.023	0.127	0.101
%N	461.2	3.568	0.036	0.165
C:N	136.7	0.928	0.406	0.049
% Mud	325.0	2.376	0.098	0.117
Depth	157.57	1.078	0.342	0.057

Table 4. Results from the distance-based linear modeling (DISTLM) of environmental variables with annelid functional trait composition in Norfolk Canyon axis, hard substrate, and slope environments.

AICc	<b>R</b> <sup>2</sup>	RSS	Selections
99.833	0.16543	2326	$\delta^{15}N$
100.27	0.25815	2068	%Corg, $\delta^{15}N$
100.8	0.23825	2123	δ <sup>15</sup> N, C:N
100.97	0.1166	2463	C:N
101.07	0.22782	2153	$\delta^{15}$ N, Depth
101.32	0.10103	2506	%Corg
101.36	0.21678	2183	%Corg, %N
101.37	0.33115	1865	%Corg, $\delta^{15}$ N, %N
101.5	0.2111	2199	δ <sup>15</sup> N, %N
101.52	0.21033	2201	% Mud, $\delta^{15}N$
Total SS(trace)		2788	

# 470 Discussion

## 471 Hard substrate adjacent habitats in Norfolk Canyon

472 Hard substrate adjacent sediment communities in Norfolk Canyon differed from both canyon 473 axis and slope communities with differences based on depth and food availability (organic 474 carbon content). Similar densities were observed between hard substrate adjacent and canyon 475 axis habitats at similar depths, suggesting some canyon-specific processes may be influencing 476 both habitats. Norfolk Canyon axis and slope communities are influenced by sediment grain size, 477 organic matter enrichment, and depth (Robertson et al., 2020) resulting in changes in 478 macrofaunal density with sediment transport and food availability, similar to other canyons 479 worldwide (Campanyà-Llovet et al., 2018). Additional environmental factors affecting the fauna 480 adjacent to canyon walls may be due to "edge effects" in hydrodynamic flow, by which different 481 amounts of material are either deposited or winnowed by the currents and internal tides, as well 482 as deposition from cliff faces that may alter the flux of nutrients delivered to sediments. Food 483 availability (inferred from organic carbon content) was low but variable adjacent to hard 484 substrates, consistent with the results from other canyons (Campanyà-Llovet et al., 2018; McClain and Barry 2010). Geological composition of sediments collected at cliff bases in 485 486 Monterey Canyon, characterized by low organic carbon content and coarse grain sizes, suggest 487 that deposition is primarily from the canyon walls (McClain and Barry 2010), where sediments 488 are influenced by high mass and carbon flux adjacent to cliff faces. McClain and Barry (2010) 489 posit that there is increased deposition adjacent to cliffs but that the low carbon content in the 490 sediments is the result of increased consumption by high densities of megafauna. However, a 491 second possibility is that the organic-rich material observed in sediment traps located 15 m above 492 the sea floor is not being deposited on the seafloor but remains in suspension and is transported

493 away due to local hydrodynamics, resulting in winnowed organic-poor, coarse-grained 494 sediments. Lastly, the presence of large grain sizes at the base of canyon walls alone supports 495 increased oxygen exposure that enhances diffusion and oxidation of organic matter (Hedges and 496 Keil, 1995). Canyon walls have a large influence on flow at mid and deep (917 and 1347 m) 497 depths in Norfolk Canyon by forcing the dominant directions in flow within the canyon with 498 general bottom flow up-canyon (CSA et al. 2017) and altering sediment and organic matter 499 transport. As the hard substrates are topographically distinct locations compared to axis and 500 slope habitats, further measurements of local near-bed hydrodynamics would help elucidate the 501 effect of near-wall flows and water mass characteristics on both sediments and food supply.

502 For hard substrate adjacent sediment communities located on the north side of the 503 canyon, diversity was generally higher than at similar or deeper depths in the canyon axis, which 504 may be a function of the increased habitat heterogeneity provided by the hard substrates to 505 adjacent sediments. In addition, diversity did not differ with depth among hard substrate adjacent 506 sediments, suggesting similar influence of habitat heterogeneity on diversity across all the depths 507 in hard substrate habitats. Multiple controls on canyon infaunal diversity have previously been 508 identified, such as depth (Conlan et al. 2015), organic matter enrichment (Ingels et al. 2011, 509 Bernardino et al. 2019), disturbance regimes (Robertson et al. 2020), and seafloor topography 510 (De Leo et al. 2014, Bianchelli et al. 2010), with particular influence of slope and aspect. The 511 steep slopes provided by the canyon walls and their location along the north wall likely influence 512 the similarity in diversity. Our results were inconsistent with those of McClain and Barry (2010), 513 where diversity was depressed adjacent to cliffs and overall declined with depth within Monterey 514 Canyon; however diversity was enhanced adjacent to cliffs at their shallowest depth (595 m) 515 suggesting non-uniform environmental controls across all their sampling locations.

516 The overall difference among hard substrate adjacent sediment and canyon axis 517 communities was the result of high dissimilarities between the hard substrate adjacent sediments 518 and the 190 m and 800 m canyon axis communities. While the 190 m canyon axis communities 519 were located at the head of the canyon >10 km from all other sampling locations (Figure 1), both 520 the 190 m and 800 m locations were typified by lower mud content than any of the hard substrate 521 adjacent habitats. Robertson et al. (2020) observed that communities at 800 m within the axis of 522 Norfolk Canyon are severely disturbed with high abundances of opportunistic taxa Capitellidae 523 and Cirratulidae (Pearson and Rosenberg, 1978) and located in an area of high water column 524 turbidity (CSA et al., 2017), sediment deposition, and organic enrichment. Higher organic 525 carbon and mud content was observed at the sampling location closest to the 800 m axis site 526 (Figure 1, D679-1), suggest some influence of the turbidity plume extending across the canyon to 527 the edges. High water column turbidity that occurs at 800 m depth can extend upwards to 700 m, 528 with moderate levels up to 500 m depth (CSA et al. 2017) supporting our results. McClain and 529 Barry (2010) hypothesized that cliff-adjacent sediments are experiencing high levels of 530 disturbance through increased bioturbation by megafauna, resulting in reduced macrofaunal 531 evenness, species richness, body size, and a lack of tube-building taxa and amphipods near cliff 532 faces. Although we have no data for biomass or macrofauna size estimates, the increased 533 diversity of taxa, presence of tube-builders and amphipods, and no dominance of opportunistic 534 taxa suggests disturbance near Norfolk Canyon hard substrates may only be moderate. Given 535 there is increasing evidence that no two canyons are alike (Cunha et al., 2011), comparisons 536 between Monterey Canyon and Norfolk Canyon may be limited; however, the results of McClain 537 and Barry (2010) provide the only insight into other canyon hard substrate adjacent sediment 538 communities. Monterey Canyon and Norfolk Canyon are morphologically and geologically

539 different and likely have different particulate organic carbon regimes due to regional differences. 540 McClain and Barry (2010) sampled within multiple sections of the larger canyon complex, with 541 their shallowest station (Soquel Canyon, 595 m) exhibiting contrasting community patterns with 542 distance from cliff faces compared to their deeper stations. Their sampling locations were at the 543 bases of cliffs where there were large expanses (>100 m) of soft-sediments. In contrast, hard 544 substrate adjacent sediments from Norfolk Canyon were collected opportunistically, typically in 545 small patches of sediment along the canyon walls or large boulders. The contrasting results 546 among the Monterey Canyon stations may reflect a higher variation in the hydrodynamic 547 regimes and sediment transport among Monterey Canyon stations than among our study 548 locations (Maier *et al.*, 2019) where there was high similarity among all depths.

549 Submarine canyons support distinct and functionally different annelid communities 550 compared to the adjacent slope, contributing to our assessment that canyon-specific processes are 551 the primary drivers influencing infaunal communities. Organic carbon content was one of the 552 key components explaining both functional, as well as community, assemblages, again 553 highlighting the importance of canyons acting as conduits and concentrators of organic matter. 554 As many of the functional traits examined here were feeding characteristics (mode, location), the 555 amount of food content in the sediments is a natural explanatory parameter. Despite lower 556 organic carbon content, hard substrate adjacent habitats were dominated by deposit feeders 557 which require organic matter to survive. Norfolk Canyon axis sediments are known to contain 558 high quality organic matter based on pigment analysis (CSA et al., 2017) and may provide the 559 nutritional support for hard substrate adjacent communities. While corresponding quantitative 560 observations on the Norfolk Canyon megafaunal communities are unavailable, the different 561 topography adjacent to hard substrates in Norfolk Canyon compared to Monterey Canyon

562 presents a lower likelihood of high densities of megafauna consuming organic matter resulting in 563 the low %Corg observed, supported by our community results. Sediment  $\delta^{15}N$  represents the 564 quality of the food available and higher values were the primary driver for separating all canyon (axis and hard substrate) from slope functional assemblages. Higher  $\delta^{15}$ N values occurring within 565 566 the canyon suggests increased reworking of organic material. However, the similarity among 567 hard substrate adjacent and canyon axis functional groups may be a result of assessing only 568 annelid communities. Annelids represented 58-84% of hard substrate adjacent communities, and 569 only 43-78% of canyon axis communities, leaving a large portion of the taxa and their functional 570 role unassessed. For example, Thyasiridae bivalves, known to contain chemoautotrophic 571 endosymbionts (Dando et al. 1994) and occupy organic-rich sediments, had high abundances at 572 the 800 m canyon axis location and were also present in some hard substrate sediments, would 573 add to the overall functional diversity. Additional assessment of feeding niche specialization by 574 non-polychaete taxa will likely enhance our understanding of the functional role of both hard 575 substrate adjacent and canyon axis habitats.

576 Although sampling was limited, differences between hard substrate adjacent sediment 577 communities on the north side and the south side of Norfolk Canyon may be an indicator of 578 localized differences in the hydrodynamic conditions. Anticyclonic circulation has been 579 observed in Baltimore Canyon (Hunkins, 1988) and other submarine canyons (Durrieu de 580 Madron, 1994; She and Klinck, 2000) resulting in differing directions in flow on opposite sides 581 of a canyon. Spatially variable topography and related hydrodynamic regimes (e.g. current 582 speed) on different sides of a submarine canyon likely result in differences in sediment 583 deposition between inner and outer bends, analogous to river environments. . High current 584 velocities have been reported from Norfolk Canyon (CSA et al., 2017; Hecker et al., 1983) and

585 long-term in situ measurements of hydrodynamic flow indicated that canyon walls have a large 586 influence on flow at mid- (917 m) and deep-canyon (1347 m) depths (CSA et al., 2017). Lower 587 proportions of surface feeders, density, diversity, and mud content suggest that the south side of 588 Norfolk Canyon experiences higher current speeds than the north side or may be receiving 589 sediment from a different source. Comparable data from Monterey Canyon indicated that organic 590 carbon content and grain size composition differed between sides of the canyon (McClain and 591 Barry, 2010), supporting potential hydrodynamic differences, although abundance and diversity 592 were similar. However, additional replicate sampling would be required to fully assess for 593 differences in biological and environmental parameters.

594

# 595 <u>Within-canyon and regional biodiversity</u>

596 Sediment communities adjacent to hard substrates contribute substantially to the 597 biodiversity present in Norfolk Canyon. Given the limited and opportunistic sampling of hard 598 substrate adjacent habitats, the slope of the rarefaction curves suggest much higher biodiversity 599 is as yet discovered from these habitats. Despite the slightly lower sampling effort for hard 600 substrate adjacent habitats (13 cores) versus the canyon axis (19 cores), a higher number of taxa 601 were encountered in sediments adjacent to hard substrate habitats. Spatial turnover of taxa was 602 also high among canyon communities. Within hard substrate adjacent habitats, communities only 603 shared 12% of taxa across the entire depth range. These results further suggest the presence of 604 different environmental niches adjacent to hard substrates, given that individual taxa 605 preferentially occupy areas with a specific range of sediment biogeochemical parameters. While 606 previous studies on canyon hard substrates have focused on the epi-megafaunal communities 607 (e.g. deep-sea corals), our results highlight that they influence adjacent sediments to support

608 distinct communities, although the scale of influence is yet unknown for Norfolk Canyon. The 609 influence of hard substrate habitats on adjacent sediments presented here is consistent with 610 results from deep-sea coral habitats (Bourque and Demopoulos, 2018; Demopoulos et al., 2014), 611 where adjacent sediment communities differed from other regional soft-sediment communities. It 612 should be noted that our analysis is at the family level and higher, providing a very conservative 613 estimate of the beta diversity within the Norfolk Canyon region. Thus beta diversity may be 614 higher than represented here, however identification beyond family level would be required to 615 confirm. There are an estimated 9500 submarine canyons worldwide (Harris et al. 2014), many 616 of which contain steep walls and sediment habitat suitable for infauna at their base. The 617 increased diversity associated with hard substrate adjacent habitats observed in Norfolk Canyon 618 suggests that the biodiversity of submarine canyons is underestimated, with these additional 619 heterogeneous habitats contributing significantly to both within-canyon and regional 620 biodiversity.

621

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cores used for seur	ment geochennear allarysis,	indicates grain size analysis of the sediment geochemical core.						
Date	Station	Latitude	Longitude	Depth (m)	MF	SC	Group	
2-May-2013	ROV-2013-RB-679-1	37.0509	-74.6300	688	2	1	Hard Substrate North	
5-May-2013	ROV-2013-RB-680-1	37.0593	-74.5809	443	1	1	Hard Substrate North	
5-May-2013	ROV-2013-RB-680-2	37.0549	-74.5739	585	2	1	Hard Substrate North	
11-May-2013	ROV-2013-RB-685-1	37.0500	-74.5140	1342	1	1	Hard Substrate North	
11-May-2013	ROV-2013-RB-685-2	37.0508	-74.5148	1273	1	1	Hard Substrate North	
11-May-2013	ROV-2013-RB-685-3	37.0516	-74.5174	1252	1	1	Hard Substrate North	
13-May-2013	ROV-2013-RB-686-1	37.0590	-74.6020	482	1	1	Hard Substrate North	
14-May-2013	ROV-2013-RB-687-1	37.0604	-74.5787	400	1	1	Hard Substrate North	
18-May-2013	ROV-2013-RB-691-1	37.0316	-74.6340	451	1	1	Hard Substrate South	
18-May-2013	ROV-2013-RB-691-2	37.0327	-74.6370	419	1	1	Hard Substrate South	
18-May-2013	ROV-2013-RB-691-3	37.0316	-74.6342	450	1	1	Hard Substrate South	
19-Sep-2012	NF-2012-159	37.0944	-74.7472	196	1	1	Canyon 190m	
11-May-2013	RB-2013-046	37.0948	-74.7466	195	1	1*	Canyon 190m	
11-May-2013	RB-2013-047	37.0948	-74.7466	195	1	1	Canyon 190m	
11-May-2013	RB-2013-048	37.0948	-74.7466	195	1	1	Canyon 190m	
19-Sep-2012	NF-2012-162	37.0760	-74.6612	573	1	1	Canyon 550m	
11-May-2013	RB-2013-043	37.0760	-74.6606	559	1	1*	Canyon 550m	
11-May-2013	RB-2013-044	37.0760	-74.6606	557	1	1	Canyon 550m	
11-May-2013	RB-2013-045	37.0760	-74.6606	558	1	1	Canyon 550m	
20-Sep-2012	NF-2012-164	37.0429	-74.6292	819	1	1	Canyon 800m	
10-May-2013	RB-2013-040	37.0427	-74.6292	805	1	1*	Canyon 800m	
10-May-2013	RB-2013-041	37.0428	-74.6292	803	1	1	Canyon 800m	
10-May-2013	RB-2013-042	37.0428	-74.6293	804	1	1	Canyon 800m	
28-Sep-2012	NF-2012-192	37.0387	-74.5799	1133	1	1	Canyon 1110m	
10-May-2013	RB-2013-038	37.0386	-74.5799	1110	1	1*	Canyon 1110m	
10-May-2013	RB-2013-039	37.0387	-74.5800	1110	1	1	Canyon 1110m	
15-May-2013	RB-2013-077	37.0388	-74.5796	1108	1	1	Canyon 1110m	

Supplemental Table 1. Location information for all hard substrate adjacent cores collected via ROV and canyon axis and adjacent slope cores collected via box core. MF indicates the number of cores used for macrofaunal analysis; SC indicates the number of cores used for sediment geochemical analysis; \* indicates grain size analysis of the sediment geochemical core.

15-May-2013	RB-2013-078	37.0335	-74.4504	1622	1	1*	Canyon 1600m
18-May-2013	RB-2013-082	37.0334	-74.4503	1619	1	1*	Canyon 1600m
18-May-2013	RB-2013-083	37.0334	-74.4503	1620	1	1*	Canyon 1600m
24-Sep-2012	NF-2012-181	37.0234	-74.6452	188	1	1	Slope 190m
11-May-2013	RB-2013-049	37.0231	-74.6458	187	1	1*	Slope 190m
11-May-2013	RB-2013-050	37.0245	-74.6473	187	1	1	Slope 190m
11-May-2013	RB-2013-051	37.0242	-74.6459	187	1	1	Slope 190m
24-Sep-2012	NF-2012-183	37.0156	-74.5786	550	1	1	Slope 550m
12-May-2013	RB-2013-054	37.0158	-74.5782	549	1	1*	Slope 550m
12-May-2013	RB-2013-055	37.0158	-74.5782	549	1	1	Slope 550m
12-May-2013	RB-2013-056	37.0158	-74.5782	548	1	1	Slope 550m
13-May-2013	RB-2013-059	37.0090	-74.5648	790	1	1	Slope 800m
12-May-2013	RB-2013-060	37.0091	-74.5647	790	1	1	Slope 800m
14-May-2013	RB-2013-069	37.0090	-74.5650	804	1	1*	Slope 800m
14-May-2013	RB-2013-070	37.0090	-74.5650	805	1	1	Slope 800m
14-May-2013	RB-2013-071	37.0058	-74.5337	1118	1	1	Slope 1110m
15-May-2013	RB-2013-073	37.0058	-74.5337	1105	1	1*	Slope 1110m
15-May-2013	RB-2013-075	37.0059	-74.5337	1103	1	1	Slope 1110m
15-May-2013	RB-2013-076	37.0058	-74.5336	1100	1	1	Slope 1110m