

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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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 µm)
23 density, diversity and community composition, and sediment geochemical parameters including

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 heterogeneity

39

40 **Introduction**

41 Submarine canyons are morphologically complex features along continental margins,
42 providing heterogeneous habitats and acting as conduits for the transport of sediment and organic
43 matter from the productive continental shelves to food-deprived abyssal plains (Puig *et al.*,
44 2014). Habitat heterogeneity is created by the wide range of environmental conditions provided
45 by variations in topography, hydrodynamic patterns, and sediment transport processes that
46 support gradients in food resources and areas of sediment resuspension and deposition (De Leo

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; Companyà-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

70 habitats (e.g. Bourque and Demopoulos, 2018; Demopoulos *et al.*, 2014), with sedimentary areas
71 adjacent to hard substrates acting as deposition zones and containing high amounts of organic
72 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.

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.

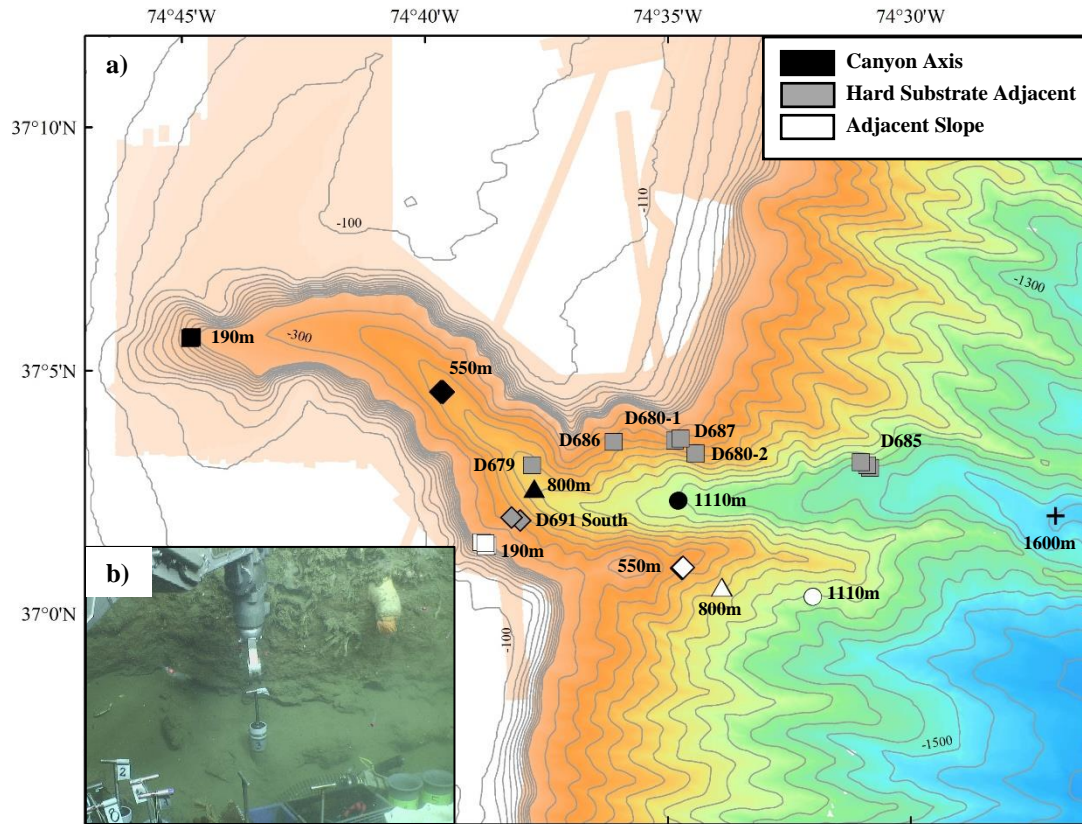
106 Here we investigate the infaunal community structure and functional composition of
107 sediment communities adjacent to hard substrates in comparison to main-axis habitats within
108 Norfolk Canyon and sediments on the adjacent continental slope by addressing the following
109 questions: 1) are sediment 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?

115

116 **Methods**

117 Sampling Procedures

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 µm) 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
132 included here to increase replication. Due to lower resolution local bathymetry available at the
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.



136

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

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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- μ m 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
159 the stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, and percent organic carbon and nitrogen.
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

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*

191 Within habitat (alpha) and between habitat (beta) diversity were examined using the total
192 number of taxa present in each core (S_p), Shannon diversity ($H' \log_e$), taxa richness estimated
193 using Marglef's index (d), and Pielou's evenness (J') based on untransformed abundance data

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

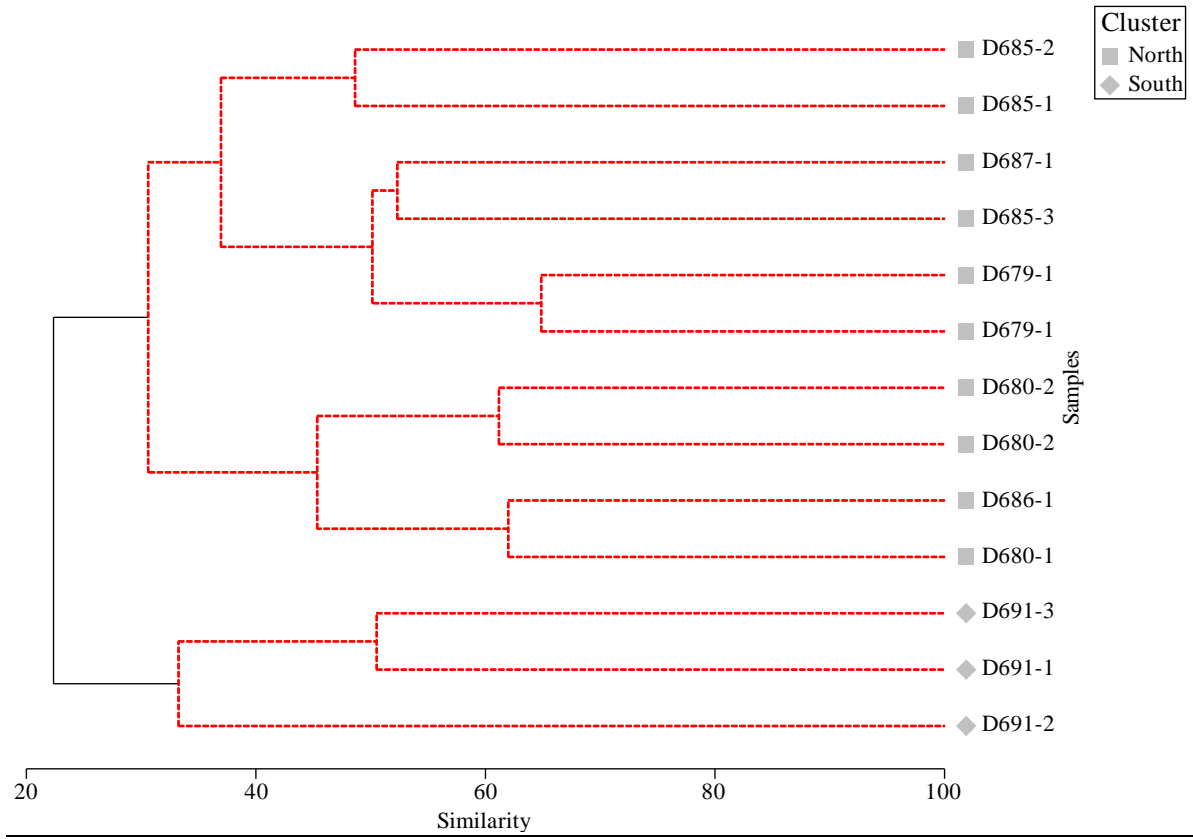
228 To further address the relationship of the environmental variables to the multivariate
229 community and functional composition data, distance-based linear modeling (DistLM) and
230 distance-based redundancy analysis (dbRDA) were performed using the PERMANOVA+ add on
231 package. DistLM performs 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
236 ($\delta^{13}\text{C}$), stable nitrogen isotope composition ($\delta^{15}\text{N}$), and the carbon to nitrogen ratio (C:N). The
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.

239

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



258

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

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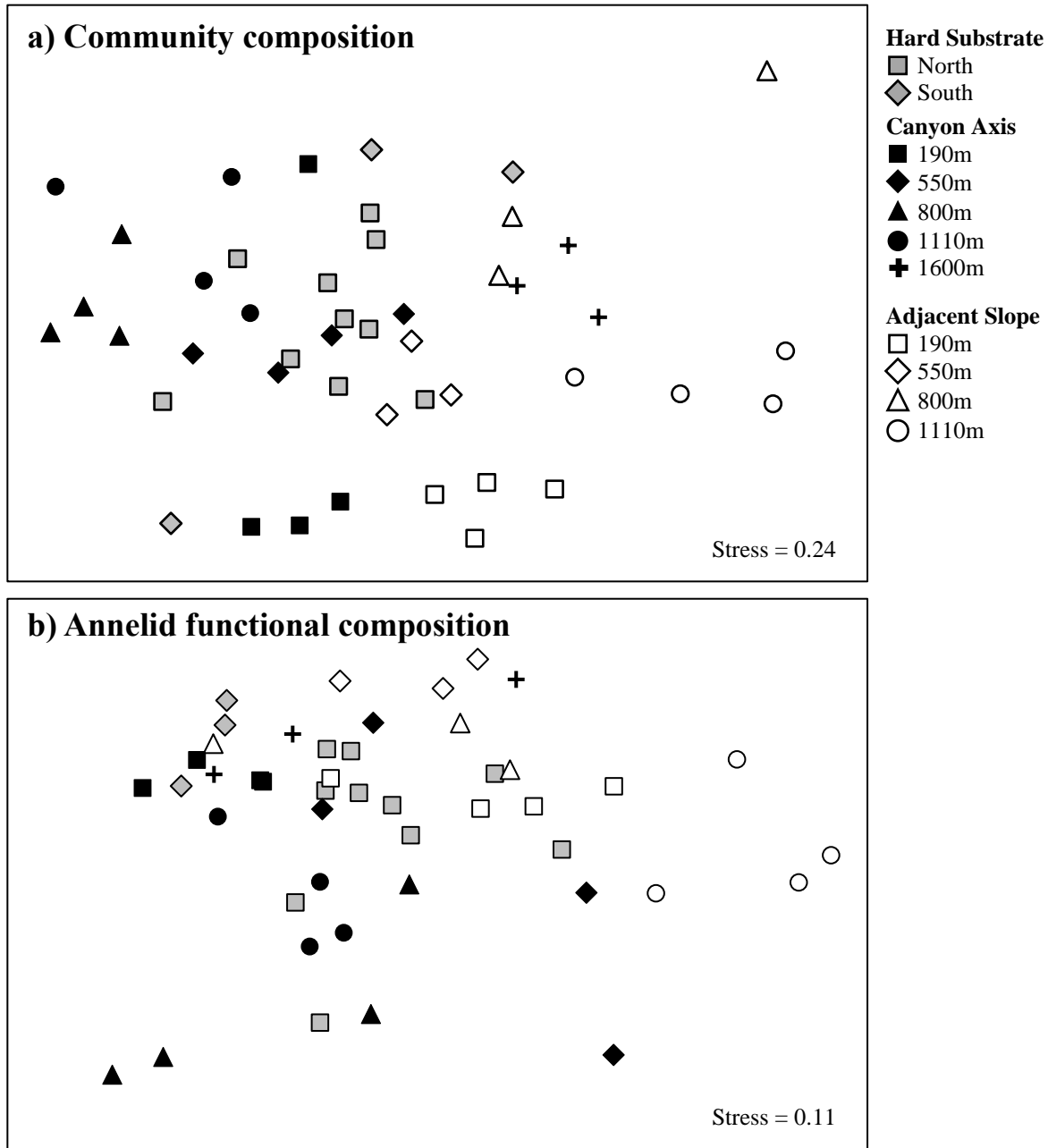
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271 Figure 3. Non-metric multidimensional scaling of cores collected adjacent to hard substrate
 272 habitats (grey symbols), in the canyon axis (black) , and on the adjacent slope (white) a) based
 273 on Bray-Curtis similarities of square-root transformed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

275

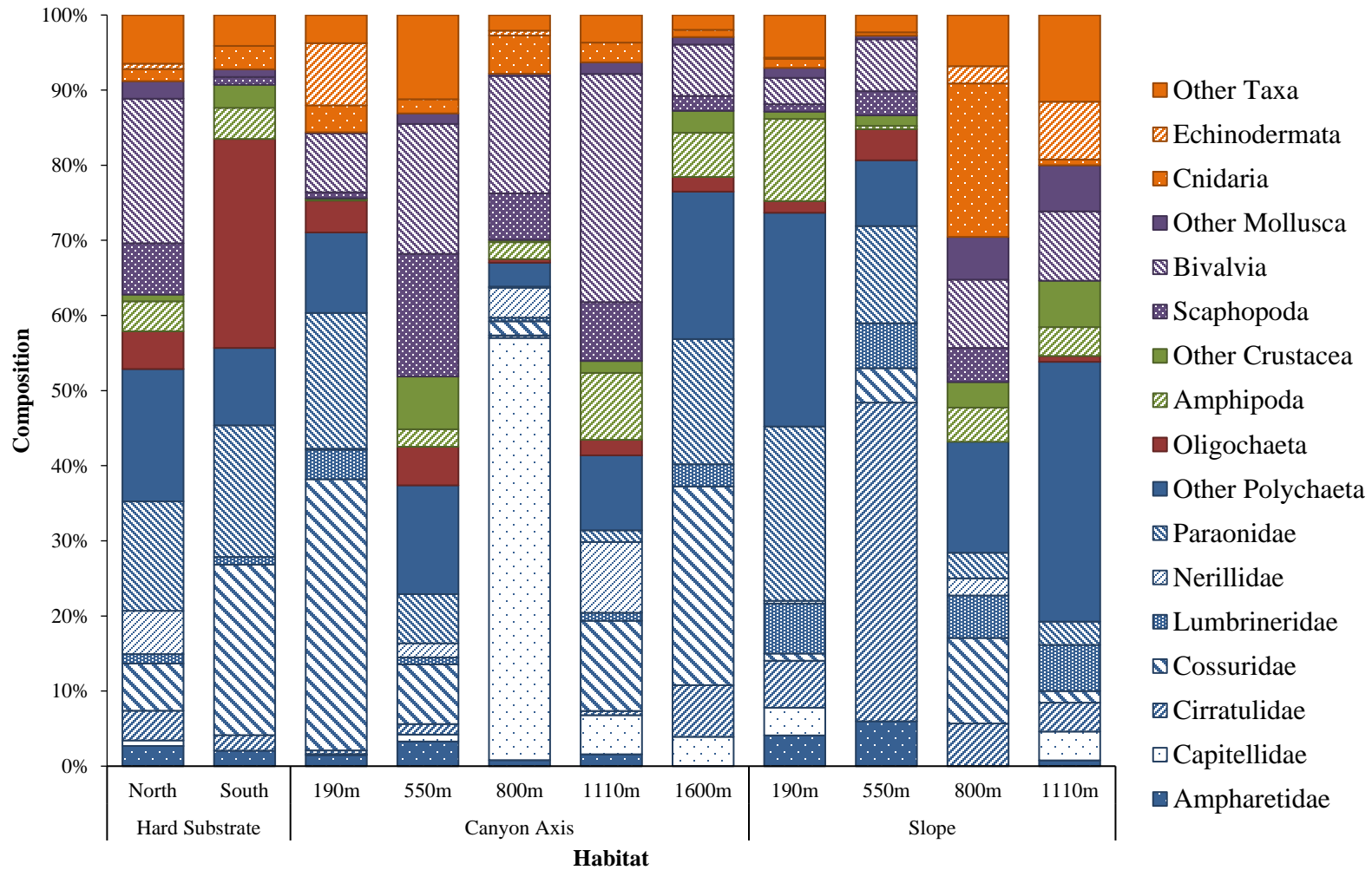
276 oligochaetes (5.0%) (Figure 3). The South cluster was characterized by high proportions of
277 Cossuridae (22.7%) and Paraonidae (17.5%, Polychaeta) and oligochaetes (27.8%), but lower
278 proportions of molluscs (2.1%) (Figure 4).

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, $F_{1-11}=1.93$, $p=0.19$) 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 , $\rho=-0.36$, $p=0.29$).

293

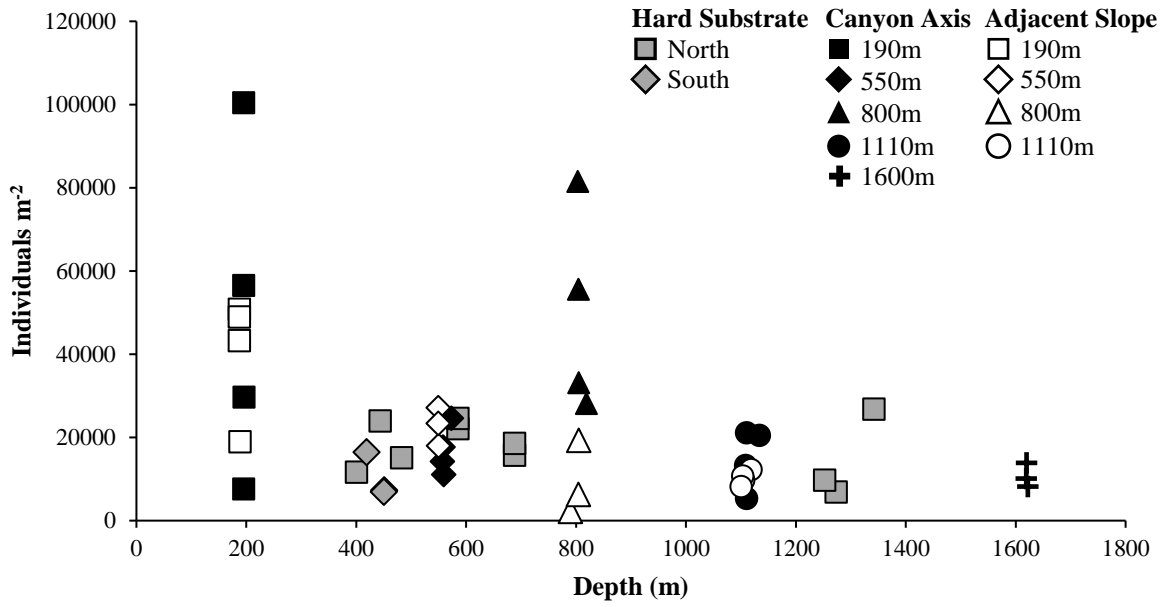
294 Hard substrate adjacent sediment functional composition

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



299

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



302

303 Figure 5. Scaled raw macrofaunal density in hard substrate adjacent, canyon axis, and slope
 304 sediments.

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

Habitat	N	Density	0-2 cm	2-5 cm	5-10cm	d	J'	H'(log _e)	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

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

325 living habit

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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, $\rho=0.88$, $p=0.001$).

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 composition

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.

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

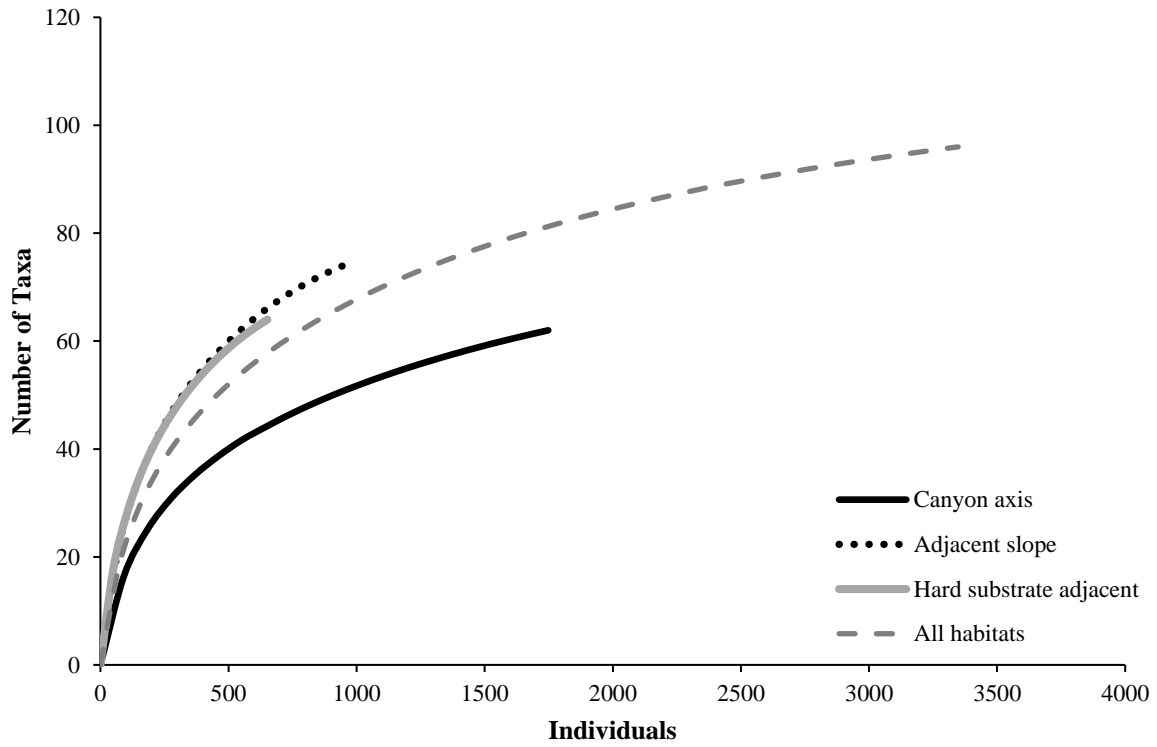
381 There was high beta diversity among hard substrate adjacent sediment habitats, canyon
382 axis, and slope sediments (Figure 8). Canyon axis, slope, and hard substrate adjacent sediment
383 habitats shared 38 taxa (38.8%), while 31 taxa were shared among any two habitats (31.6%) and
384 29 taxa (29.6%) 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, $\rho=0.656$, $p=0.0028$ 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).

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398 Figure 7. Rarefaction of hard substrate adjacent, canyon axis, and adjacent slope macrofaunal
 399 communities.

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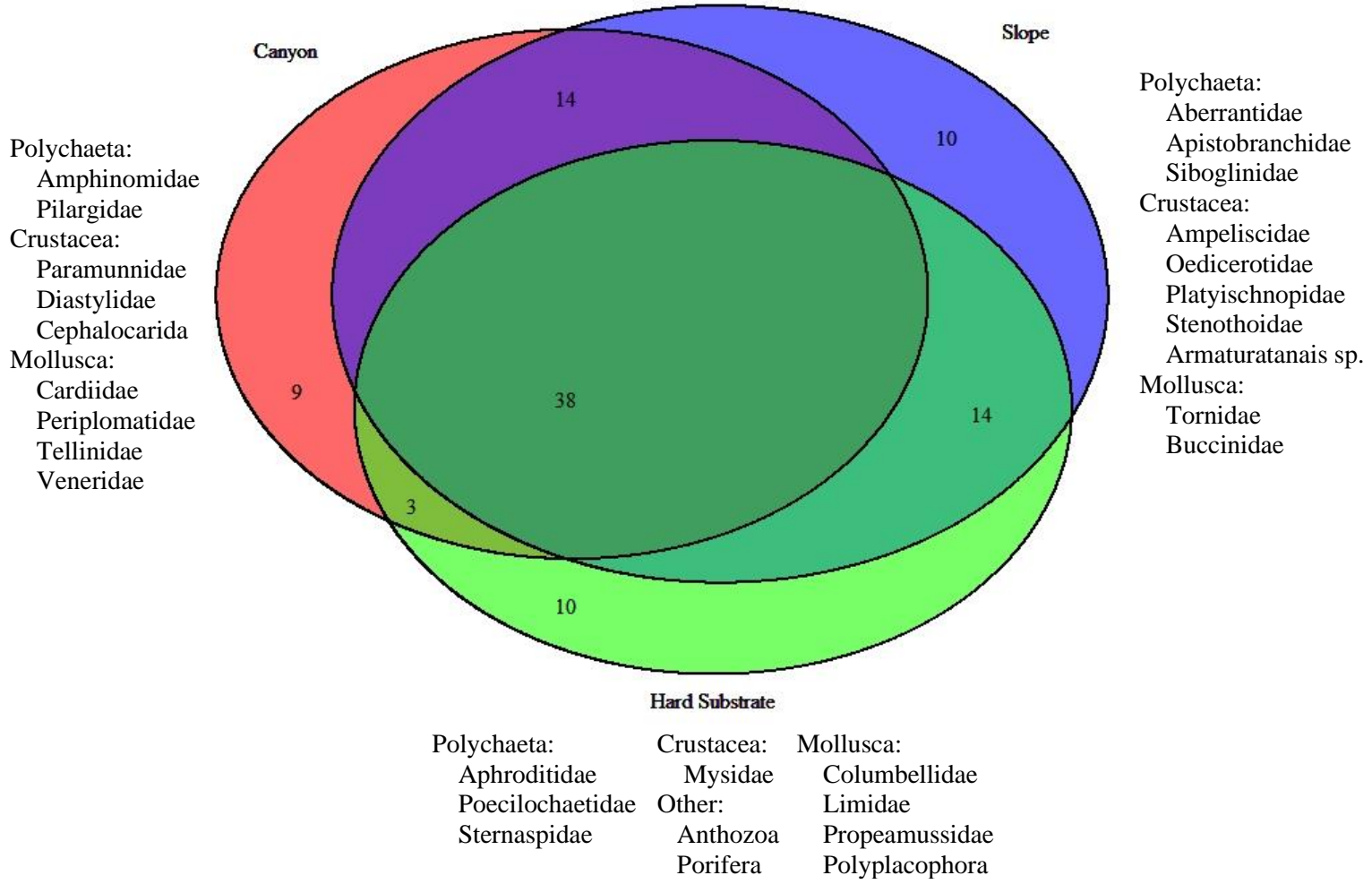
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Figure 8. Beta diversity of hard substrate, canyon axis, and slope habitats. Listed taxa are those exclusive to a single habitat.

414 Table 2. Mean sediment geochemical values for hard substrate adjacent, canyon axis, and slope
 415 habitats. Numbers in parentheses indicate the standard error of the mean.

Habitat	% Mud		$\delta^{13}\text{C}$		%Corg		$\delta^{15}\text{N}$		%N		C: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)

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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
437 (21.5%), percent mud (21.2%), or $\delta^{13}\text{C}$ (20.6%) serving as potential explanatory models.
438 Environmental variables structured annelid functional trait composition differently than the
439 macrofaunal communities. Of the seven explanatory variables only $\delta^{15}\text{N}$ composition explained a
440 significant portion (16.5%, $p=0.036$) of the variation in functional composition (Table 4). The
441 “best” model included $\delta^{15}\text{N}$ alone, while the “best” two-variable model (within 1 AICc unit of
442 the top model) included both $\delta^{15}\text{N}$ and %Corg and explained 25.8% of the variation in functional
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 $\delta^{15}\text{N}$ separates individual locations of hard substrate adjacent
446 habitats and canyon and slope communities.

Table 3. Results from the distance-based linear modeling (DISTLM) of environmental variables with macrofaunal communities in Norfolk Canyon axis, hard substrate adjacent, and slope environments.

Variable	SS(trace)	Pseudo-F	P	Proportion
$\delta^{13}\text{C}$	3033.4	1.796	0.027	0.091
%C	3869.2	2.356	0.001	0.116
$\delta^{15}\text{N}$	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 ²	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	$\delta^{13}\text{C}$
151.31	0.20614	26539	$\delta^{13}\text{C}$, %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	

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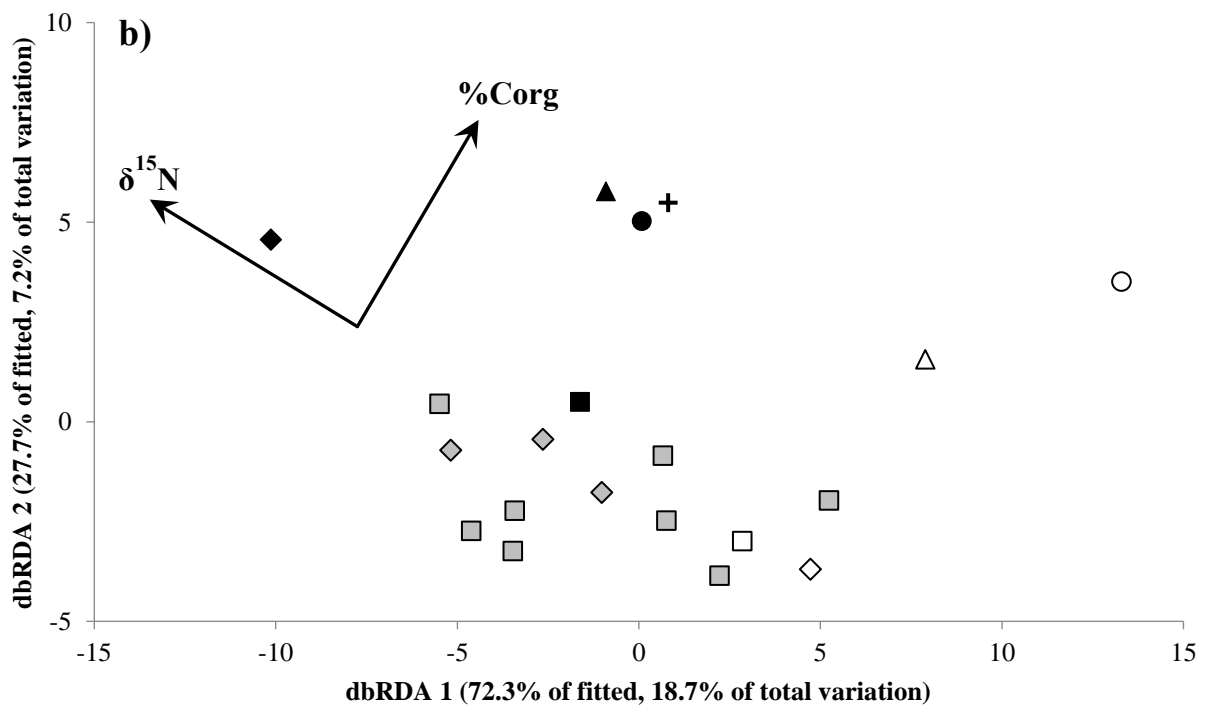
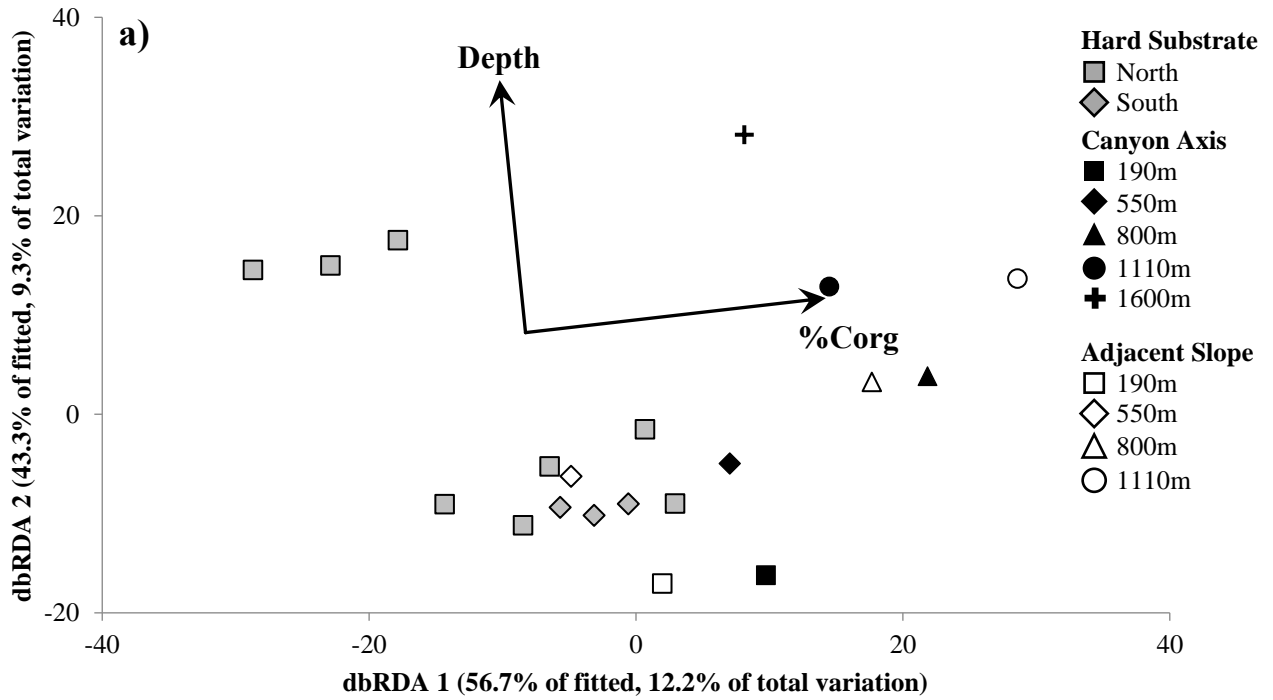
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 457 Figure 9. dbRDA of top two-variable DISTLM model of environmental variables for a)
 458 macrofaunal community; b) annelid functional composition.

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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.

Variable	SS(trace)	Pseudo-F	P	Proportion
$\delta^{13}\text{C}$	123.2	0.832	0.447	0.044
%C	187.4	1.297	0.267	0.067
$\delta^{15}\text{N}$	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

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

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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;
485 McClain and Barry 2010). Geological composition of sediments collected at cliff bases in
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 $\delta^{15}\text{N}$ represents the
564 quality of the food available and higher values were the primary driver for separating all canyon
565 (axis and hard substrate) from slope functional assemblages. Higher $\delta^{15}\text{N}$ values occurring within
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 Within-canyon and regional biodiversity

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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635

636 **References**

637 Anderson, M., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to
638 Software and Statistical Methods. PRIMER-E Ltd., Plymouth, UK.

639 Baker, K.D., Wareham, V.E., Snelgrove, P.V.R., Haedrich, R.L., Fifield, D.A., Edinger, E.N.,
640 Gilkinson, K.D., 2012. Distributional patterns of deep-sea coral assemblages in three
641 submarine canyons off Newfoundland, Canada Marine Ecology Progress Series 445, 235-
642 249.

643 Bernardino, A.F., Gama, R.N., Mazzuco, A.C.A., Omena, E.P., Lavrado, H.P., 2019. Submarine
644 canyons support distinct macrofaunal assemblages on the deep SE Brazil margin. Deep Sea
645 Research Part I: Oceanographic Research Papers 149, 103052.

646 Bourque, J.R., Demopoulos, A.W.J., Robertson, C.M., 2020. Benthic Infaunal
647 Communities of Baltimore and Norfolk Canyons. U.S. Geological Survey data release.
648 <https://doi.org/10.5066/F7H70DRH>.

649 Bourque, J.R., Demopoulos, A.W.J., 2018. The influence of different deep-sea coral habitats on
650 sediment macrofaunal community structure and function. Peerj 6, e5276.

651 Brooke, S.D., Watts, M.W., Heil, A.D., Rhode, M., Mienis, F., Duineveld, G.C.A., Davies, A.J.,
652 Ross, S.W., 2017. Distributions and habitat associations of deep-water corals in Norfolk and

653 Baltimore Canyons, Mid-Atlantic Bight, USA. *Deep Sea Research Part II: Topical Studies in*
654 *Oceanography* 137, 131-147.

655 Campanyà-Llovet, N., Snelgrove, P.V.R., De Leo, F.C., 2018. Food quantity and quality in
656 Barkley Canyon (NE Pacific) and its influence on macroinfaunal community structure.
657 *Progress in Oceanography* 169, 106-119.

658 Castella, E., Speight, M.C.D., 1996. Knowledge representation using fuzzy coded variables: an
659 example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine
660 wetlands. *Ecological Modelling* 85 (1), 13-25.

661 Charvet, S., Statzner, B., Usseglio-Polatera, P., Dumont, B., 2000. Traits of benthic
662 macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in
663 Europe. *Freshwater Biology* 43 (2), 277-296.

664 Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-
665 term ecological data. *Freshwater Biology* 31 (3), 295-309.

666 Clarke, K.R., Gorley, R.N., 2015. *PRIMER v7: User Manual/Tutorial*. PRIMER-E, Plymouth,
667 UK.

668 CSA, Ross, S.W., Brooke, S., Baird, E., Coykendall, D.K., Davies, A.J., Demopoulos, A.W.J.,
669 France, S.C., Kellogg, C.A., Mather, R., Mienis, F., Morrison, C., Prouty, N., Roark, B.,
670 Robertson, C.M., 2017. *Exploration and Research of Mid-Atlantic Deepwater hard Bottom*
671 *Habitats and Shipwrecks with Emphasis on Canyons and Coral Communities: Atlantic*
672 *Deepwater Canyons Study. Vol I. Final Technical Rept., Vol. II: Final Appendices., OCS*
673 *Study BOEM 2017-060 (Vol. I) & 061 (Vol. II)*. U.S. Dept. of the Interior, Bureau of Ocean
674 Energy Management, Atlantic OCS Region, p. 1000 p + appendices.

675 Cunha, M.R., Paterson, G.L.J., Amaro, T., Blackbird, S., de Stigter, H.C., Ferreira, C., Glover,
676 A., Hilario, A., Kiriakoulakis, K., Neal, L., Ravara, A., Rodrigues, C.F., Tiago, A., Billett,
677 D.S.M., 2011. Biodiversity of macrofaunal assemblages from three Portuguese submarine
678 canyons (NE Atlantic). *Deep-Sea Research Part II-Topical Studies in Oceanography* 58 (23-
679 24), 2433-2447.

680 De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine
681 canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the*
682 *Royal Society B-Biological Sciences* 277 (1695), 2783-2792.

683 De Leo, F.C., Vetter, E.W., Smith, C.R., Rowden, A.A., McGranaghan, M., 2014. Spatial scale-
684 dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and
685 diversity off the Main and Northwest Hawaiian Islands. *Deep Sea Research Part II: Topical*
686 *Studies in Oceanography* 104 (0), 267-290.

687 Demopoulos, A.W.J., Bourque, J.R., Durkin, A., Cordes, E.E., 2018. The influence of seep
688 habitats on sediment macrofaunal biodiversity and functional traits. *Deep Sea Research Part*
689 *I: Oceanographic Research Papers* 142, 77-93.

690 Demopoulos, A.W.J., Bourque, J.R., Frometa, J., 2014. Biodiversity and community
691 composition of sediment macrofauna associated with deep-sea *Lophelia pertusa* habitats in
692 the gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 93, 91-103.

693 Duineveld, G., Lavaleye, M., Berghuis, E., de Wilde, P., 2001. Activity and composition of the
694 benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic).
695 *Oceanologica Acta* 24 (1), 69-83.

696 Durrieu de Madron, X., 1994. Hydrography and nepheloid structures in the Grand-Rhone
697 canyon. *Continental Shelf Research* 14 (5), 457-477.

698 Escobar Briones, E., Estrada Santillán, E.L., Legendre, P., 2008. Macrofaunal density and
699 biomass in the Campeche Canyon, Southwestern Gulf of Mexico. *Deep Sea Research Part II:*
700 *Topical Studies in Oceanography* 55 (24-26), 2679-2685.

701 Folk, R.L., 1968. *Petrology of sediment rocks*. Hemphill Publishing Company, Austin, TX.

702 Gambi, C., Carugati, L., Lo Martire, M., Danovaro, R., 2019. Biodiversity and distribution of
703 meiofauna in the Gioia, Petrace and Dohrn Canyons (Tyrrhenian Sea). *Progress in*
704 *Oceanography* 171, 162-174.

705 García, R., van Oevelen, D., Soetaert, K., Thomsen, L., De Stigter, H.C., Epping, E., 2008.
706 Deposition rates, mixing intensity and organic content in two contrasting submarine canyons.
707 *Progress in Oceanography* 76 (2), 192-215.

708 Gunton, L.M., Gooday, A.J., Glover, A.G., Bett, B.J., 2015a. Macrofaunal abundance and
709 community composition at lower bathyal depths in different branches of the Whittard
710 Canyon and on the adjacent slope (3500m; NE Atlantic). *Deep Sea Research Part I:*
711 *Oceanographic Research Papers* 97 (0), 29-39.

712 Gunton, L.M., Neal, L., Gooday, A.J., Bett, B.J., Glover, A.G., 2015b. Benthic polychaete
713 diversity patterns and community structure in the Whittard Canyon system and adjacent slope
714 (NE Atlantic). *Deep Sea Research Part I: Oceanographic Research Papers* 106, 42-54.

715 Harris et al. 2014

716 Hecker, B., Logan, D.T., Gandarillas, F.E., Gibson, P.R., 1983. Megafaunal assemblages in
717 Lydonia Canyon, Baltimore Canyon, and selected slope areas. In: Observatory, L.-D.G.
718 (Ed.), *Canyon and Slope Processes Study*. Minerals Management Service.

719 Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and
720 speculative synthesis. *Marine Chemistry* 49 (2), 81-115.

721 Hunkins, K., 1988. Mean and tidal currents in Baltimore canyon. *Journal of Geophysical*
722 *Research: Oceans* 93 (C6), 6917-6929.

723 Huvenne, V.A.I., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach, V., Le Bas,
724 T.P., Wolff, G.A., 2011. A picture on the wall: Innovative mapping reveals cold-water coral
725 refuge in submarine canyon. *PloS one* 6 (12), e28755.

726 Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and its
727 relation to the quantity and quality of sedimentary organic matter in the deep Nazaré Canyon,
728 Western Iberian Margin. *Deep Sea Research Part I: Oceanographic Research Papers* 56 (9),
729 1521-1539.

730 Ingels, J., Tchessunov, A.V., Vanreusel, A., 2011. Meiofauna in the Gollum Channels and the
731 Whittard Canyon, Celtic Margin-How Local Environmental Conditions Shape Nematode
732 Structure and Function. *PloS one* 6 (5).

733 Levin, L.A., Sibuet, M., 2012. Understanding continental margin biodiversity: A new imperative.
734 *Annual Review of Marine Science* 4, 79-+.

735 Maier, K.L., Gales, J.A., Paull, C.K., Rosenberger, K., Talling, P.J., Simmons, S.M., Gwiazda,
736 R., McGann, M., Cartigny, M.J.B., Lundsten, E., Anderson, K., Clare, M.A., Xu, J., Parsons,
737 D., Barry, J.P., Wolfson-Schwehr, M., Nieminski, N.M., Sumner, E.J., 2019. Linking Direct
738 Measurements of Turbidity Currents to Submarine Canyon-Floor Deposits. *Frontiers in Earth*
739 *Science* 7 (144).

740 McClain, C.R., Barry, J.P., 2010. Habitat heterogeneity, disturbance, and productivity work in
741 concert to regulate biodiversity in deep submarine canyons. *Ecology* 91 (4), 964-976.

742 Mortensen, P.B., Buhl-Mortensen, L., Freiwald, A., Roberts, J.M., 2005. Deep-water corals and
743 their habitats in The Gully, a submarine canyon off Atlantic Canada. In: Freiwald, A.,

744 Roberts, J.M. (Eds.), Cold-water Corals and Ecosystems. Springer-Verlag, Berlin
745 Heidelberg, pp. 247-277.

746 Obelcz, J., Brothers, D., Chaytor, J., Brink, U.t., Ross, S.W., Brooke, S., 2014. Geomorphic
747 characterization of four shelf-sourced submarine canyons along the U.S. Mid-Atlantic
748 continental margin. *Deep Sea Research Part II: Topical Studies in Oceanography* 104 (0),
749 106-119.

750 Orejas, C., Gori, A., Iacono, C.L., Puig, P., Gili, J.M., Dale, M.R.T., 2009. Cold-water corals in
751 the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and
752 anthropogenic impact. *MEPS* 397, 37-51.

753 Pierdomenico, M., Gori, A., Guida, V.G., Gili, J.-M., 2017. Megabenthic assemblages at the
754 Hudson Canyon head (NW Atlantic margin): Habitat-faunal relationships. *Progress in*
755 *Oceanography* 157 (Supplement C), 12-26.

756 Puig, P., Palanques, A., Martín, J., 2014. Contemporary Sediment-Transport Processes in
757 Submarine Canyons. *Annual Review of Marine Science* 6 (1), 53-77.

758 Quattrini, A.M., Nizinski, M.S., Chaytor, J.D., Demopoulos, A.W.J., Roark, E.B., France, S.C.,
759 Moore, J.A., Heyl, T., Auster, P.J., Kinlan, B., Ruppel, C., Elliott, K.P., Kennedy, B.R.C.,
760 Lobecker, E., Skarke, A., Shank, T.M., 2015. Exploration of the Canyon-Incised Continental
761 Margin of the Northeastern United States Reveals Dynamic Habitats and Diverse
762 Communities. *PloS one* 10 (10).

763 R Development Core Team, 2018. R: A language and environment for statistical computing. . R
764 Foundation for Statistical Computing Vienna, Austria.

765 Robertson, C.M., Demopoulos, A.W.J., Bourque, J.R., Mienis, F., Duineveld, G.C.A., Lavaleye,
766 M.S.S., Koivisto, R.K.K., Brooke, S.D., Ross, S.W., Rhode, M., Davies, A.J., 2020.

- 767 Submarine canyons influence macrofaunal diversity and density patterns in the deep-sea
768 benthos. *Deep Sea Research Part I: Oceanographic Research Papers* 159, 103249.
- 769 She, J., Klinck, J.M., 2000. Flow near submarine canyons driven by constant winds. *Journal of*
770 *Geophysical Research: Oceans* 105 (C12), 28671-28694.
- 771 Zar, J.H., 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, NJ.

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.

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

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