Influence of an oxygen minimum zone and macroalgal enrichment on benthic megafaunal community composition in a NE Pacific submarine canyon

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Abstract :

Megafaunal diversity in the deep sea shows a parabolic pattern with depth. It can be affected by factors such as low oxygen concentration, which suppresses diversity, or the presence of submarine canyons, which enhances it. Barkley Canyon, located off the west coast of British Columbia, Canada, is a submarine canyon that extends from the continental margin (200 m) into the deep ocean (2,000 m). This canyon receives drift kelp from shoreline kelp forests and contains an oxygen minimum zone (OMZ) at 500 to 1,500 m depth. Our study investigated the abundance and diversity of epibenthic megafauna over a range of depths (200–2,000 m) and oxygen concentrations (0.5–5.0 ml/L) within Barkley Canyon, as well as changes in abundance near detrital kelp. Video was collected using the remotely operated vehicle ROPOS along seven 1-km cross-canyon (i.e., across the axis of the canyon) transects and three 40-m perpendicular cross-transects over kelp. Taxonomic groups were associated with depth, temperature, and the presence of pebbles. The OMZ restricted pennatulids, and edge effects along OMZ boundaries were observed for ophiuroids. The geomorphology of the sea floor affected the distribution of taxa across the canyon, with Porifera mainly found along the walls and Echinoidea within the canyon axis. Expected richness exhibited a bimodal pattern, peaking at 300 and 2,000 m, possibly due to the combined effect of the OMZ and the submarine canyon. Echinoidea aggregated near drift kelp at 200 and 300 m. We found that faunal communities in Barkley Canyon were influenced by several confounded factors including depth, oxygen and substrate. Understanding faunal patterns is paramount with increased exploitation and a changing climate.

Keywords : Barkley Canyon, benthic surveys, British Columbia, kelp detritus, oxygen minimum zone, submarine canyon

1. Introduction

Submarine canyons are steep-walled valleys cutting into continental margins. Over 9,000 canyons have been currently identified worldwide with 2,000 in the North Pacific Ocean (Harris et al. 2014). Canyons can be a source of habitat heterogeneity in the deep sea, resulting from fluctuating physical processes (Puig et al. 2014; Callow et al., 2014), food availability (Vetter, 1994; Harrold et al. 1998; Vetter & Dayton 1999), and/or oxygen levels (Levin 2003).

Physical processes, such as internal waves, turbidity currents, and upwelling and downwelling can be enhanced in canyons compared to the adjacent continental slope (Callow et al. 2014) and can alter the canyon habitat through funneling sediment and organic detritus from the shelf (Harrold et al. 1998; Vetter & Dayton 1998; Vetter & Dayton 1999; Puig et al. 2014), erosion, or sediment re-suspension (reviewed in Callow et al. 2014). Increased input of organic detritus from the shelf can enhance benthic organic matter to a food-limited environment (Harrold et al. 1998; Vetter & Dayton 1998; Vetter & Dayton 1999).

In general, on the continental slope, faunal abundance and biomass decrease with depth from the shelf break (200 m) to the abyssal plains (4000 m) as a result of the exponential decrease in phytodetrital input from surface waters (Rex et al. 2006). Other factors that can regulate the slope benthic community include oxygen concentration (Gooday et al. 2010) and topography (McClain & Barry 2010). Submarine canyons

typically exhibit increased biomass and biodiversity relative to non-canyon habitats at similar depths (Vetter & Dayton 1999; De Leo et al. 2010; McClain & Barry 2010; Vetter et al. 2010). In canyons, different types of substrates and the **presence of exposed bedrock** can support high species diversity, with deposit feeders and scavengers exploiting soft-sedimented areas and sessile filter feeders utilizing hard substrate along the canyon walls (Vetter & Dayton 1998, Huvenne et al. 2011). Amaro et al. (2016) proposed that cliff habitats in Whittard Canyon, Northeast Atlantic, hosted high megafauna diversity because of enhanced food availability for filter feeders and reduced sedimentation. Similarly, in Monterey Canyon, California, influx of organic debris was greater, and megafaunal density higher, on the face of the cliff than at a distance from the cliff (McClain & Barry 2010).

Fluctuations in oxygen level, such as at Oxygen Minimum Zones (OMZs), can also increase habitat heterogeneity along the continental margin (Levin 2003). An OMZ is a region with stable low oxygen, where oxygen concentration drops below 0.5 ml L^{-1} (Levin 2003). OMZs impinge on continental margins at intermediate depths between 100 and 1400 m and occur in areas of high surface productivity (Levin et al. 2001). These low-oxygen areas are sporadic in the deep sea, where oxygen is usually saturated at 5-6 ml L^{-1} . Globally, OMZs occupy $1,148,000 \text{ km}^2$, and most occur in the Indian Ocean (59%) and the eastern Pacific Ocean (31%) (Helly & Levin 2004). OMZs are generated where organic material sinks and is then degraded through aerobic processes, leading to a reduction in oxygen concentration. Weak water circulation and oxygen-depleted source waters enhance OMZs, and variability in productivity and circulation affects the thickness and magnitude of the OMZ (Helly & Levin 2004). Given the projected increase

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116 in sea surface temperature leading to enhanced ocean stratification, OMZs are predicted
117 to increase in size and intensity in the future (Helly & Levin 2004; Diaz & Rosenberg
118 2008).

119 Low oxygen influences the abundance and composition of epibenthic
120 communities in the deep sea. **For example, the density of meiofauna increases in**
121 **OMZs, while both macrofauna and meiofauna exhibit low species richness and**
122 **dominance of particular taxa** (Levin & Gage 1998; Levin et al. 2001). Density and
123 diversity of megafauna decreases within the core of the OMZ, likely because of low
124 tolerance and lack of adaptation to low oxygen. In the sediments in OMZs, oxygen levels
125 below 0.05 ml L⁻¹ were associated with increased concentrations of phytodetritus and
126 organic matter, as well as preservation of organic material (Cowie & Hedges 1992; Levin
127 2003; Gooday et al. 2010). However, this rich food source is not always readily available
128 for megafauna that are unable to adapt to the low oxygen levels. Megafaunal densities
129 can be higher along the upper and lower boundaries of the OMZ than within it, likely
130 because of an interaction between the release from low oxygen and the presence of high
131 organic matter (Levin 2003).

132 In the eastern Pacific Ocean, along the west coast of Canada and the United
133 States, OMZs are maintained by upwelling which leads to high productivity and the
134 presence of older, oxygen-poor source water with low rates of replenishment (Wyrtky
135 1966; Reid & Mantyla 1978). An OMZ is found along the Northeastern Pacific,
136 impinging on submarine canyons. Seasonal variability in the direction of currents
137 influences patterns in upwelling in the area. In winter, the sea surface current runs
138 northwest, parallel to the shore and towards Alaska. In April and May, the current, **forced**

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3 139 **by a seasonal change in wind, reverses direction** to the southeast towards California
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5 140 (Freeland et al. 1984), causing upwelling on the continental margin along the coast of
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8 141 Vancouver Island **throughout the summer into early fall** (Allen et al. 2001). Upwelling
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10 142 brings nutrients to the surface, increases productivity, and ultimately contributes to the
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12 143 formation of an OMZ (Freeland et al. 1984). A number of studies have noted an increase
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14 144 in upwelling intensity and severity and the number of hypoxic events, resulting in long-
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16 145 term decreasing dissolved oxygen concentrations in the area (Bograd et al. 2008;
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18 146 Whitney et al. 2007).

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22 147 Barkley Canyon is a submarine canyon found within the area affected by the
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24 148 OMZ in the Northeastern Pacific Ocean. In addition to the influence of the OMZ, the
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26 149 proximity of the canyon to the coast (~100 km) could affect food supply due to a
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28 150 potential influx of kelp macrodetritus from near coastal kelp forests (Vetter 1994; Harrold
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30 151 et al. 1998). We hypothesized that the canyon will display a low diversity and abundance
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32 152 of megafauna within the OMZ compared to the upper continental slope but that
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34 153 phytodetritus deposits will locally enhance abundance of species adapted to low oxygen
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36 154 concentrations. The combination of these two processes may result in an unusual spatial
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38 155 pattern in abundance and diversity with depth. In this study: 1) we quantified broad-scale
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40 156 patterns in epibenthic megafauna (organisms visible in still images, usually > 1 to 2 cm)
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42 157 in relation to depth (200 m to 2000 m) and oxygen concentration (0.5-5 ml L⁻¹)
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44 158 throughout Barkley Canyon; and 2) based on the hypothesis of enhanced organic detritus
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46 159 in submarine canyons, we investigated fine-scale spatial changes in mobile epibenthic
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48 160 megafauna in the presence of macroalgal detritus in Barkley Canyon.
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161 **2. Materials and Methods**

162 *2.1 Study area*

163 Barkley Canyon is a submarine canyon along the Northeast Pacific continental
164 margin ~100 km from the west coast of Vancouver Island, British Columbia, Canada
165 (Fig. 1). The canyon is located along the edge of the Cascadia subduction zone, with the
166 head at the continental break and extending into the continental slope from 200 m to
167 >2000 m depth. The canyon is ~42 km long along its longitudinal axis, and its width is
168 narrower at the head (~1 km) widening to a maximum of 7 km at the continental slope.
169 The continental margin off the coast of Vancouver Island that includes Barkley Canyon is
170 located in the North Pacific oxygen minimum zone (OMZ) characterized by oxygen
171 concentrations below 0.5 ml L⁻¹ (Levin 2003; Juniper et al. 2013).

172 *2.2 Benthic video surveys*

173 We conducted benthic video surveys using the remotely-operated vehicle (ROV)
174 ROPOS aboard the *R/V Falkor* (Schmidt Ocean Institute) on 4-19 September 2013.
175 ROPOS was equipped with forward-facing and downward-facing high-definition cameras
176 (Insite Pacific Zeus-Plus 1090i HD and Insite Pacific Mini Zeus 1080i HD, respectively)
177 and **each camera was equipped** with lasers calibrated at 10 cm apart. The ROV
178 performed 7 1-km transects **approximately along isobaths at different target depths**
179 within Barkley Canyon (200 to 2000 m), surveying a total of 6906 m of the seafloor (Fig.
180 1, Table 1). The ROV maintained an altitude of ~1 m above the seafloor during
181 transects, and is equipped with an ultra-short baseline responder (USBL) allowing its
182 precise positioning on the seafloor.

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3 183 Where drift kelp was observed on the seafloor, we conducted 2 perpendicular
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5 184 cross 40-m transects with the kelp debris at the centre (Table 2). After the 2 transects
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8 185 were completed, the kelp debris was collected and blade length measured onboard ship.
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10 186 Kelp were frozen and subsequently weighed in the laboratory. Transects that were longer
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12 187 than 40 m were shortened to 40 m (e.g. 200-m transect).
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16 188 *2.3 Environmental Data*

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18 189 ROPOS was equipped with a CTD profiler (SBE 19plusV2) that recorded oxygen,
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20 190 temperature, and salinity **continuously throughout the dive**. Based on the CTD data, we
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22 191 identified the location of the oxygen minimum zone, as the depths over which oxygen
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24 192 was below 0.5 ml L⁻¹.
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27 193 *2.4 Video data processing*

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29 194 For each 1-km transect, frame-grabs were extracted from the video of the
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31 195 downward-facing camera at 1-minute intervals (average distance between adjacent
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33 196 frame-grabs: 8 ± 1 m). Images were discarded if they were blurry, if the ROV was too
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35 197 high off the seafloor to distinguish organisms, or if there were other obstructions, such as
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37 198 large fish. Each image was cropped to cover an area of 1 m x 1 m, centered at the
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39 199 brightest portion of the image. Since the ROV was in constant motion, its angle varied
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41 200 between transects and the illuminated area would shift with different frame-grabs. If the
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43 201 image surface area was $< 1 \text{ m}^2$, the surface area of the maximum height and width in the
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45 202 lit portion of the image was used (range 0.31-1.01 m²; 125 images $< 1 \text{ m}^2$). In total, 971
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47 203 images were extracted and 860 used for analysis (Table 1). For each 40-m cross transect,
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49 204 the entire video sequence along each segment was analyzed.
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205 All epibenthic megafauna were enumerated in each image. For the 1-km transects,
206 individuals were included if more than half of their body was within the image or, in the
207 case of sessile species, if the holdfast was in the frame. For the cross transects, all mobile
208 epibenthic megafauna were enumerated along the video transects and their position
209 relative to the kelp detritus recorded. All organisms were identified to the lowest
210 taxonomic level possible based on the images (physical samples unavailable for most
211 species). Since some species could not be identified without specimens (not collected),
212 the term ‘morphospecies’ is used in this study. Morphospecies were pooled into broader
213 taxonomic groups for the analyses (Alcyonacea, Echinoidea, Porifera, Gastropoda,
214 Crinoidea, Ophiuroidea, Pennatulacea, Hydrozoa, Actiniaria, Decapoda, Holothuroidea,
215 and Asteroidea).

216 Along each 1-km transect, qualitative observations of the substrate type were
217 made. The presence of large boulders or cobbles was recorded, as well as the appearance
218 of the sediment, for example, whether it was easily-disturbed clay, coarser grain sediment
219 or a heavily pebbled area. At the head of the canyon (transects at target depths 200-
220 600 m), we distinguished the walls and axis of the canyon based on the rate of
221 change in depth with horizontal distance throughout the entire 1-km transect. For
222 example, at target depths > 600 m, depth only varied by on average 100 m along the
223 1-km transect with the least variation at the 200 m target depth (30 m over 1 km)
224 and the most at 600 m target depth (130 m over 1 km).

225 *2.5 Data analysis*

226 Although there was some depth overlap at the shallower transects (target
227 depths: 200 m, 300 m, 400 m), the main objective of the study was to sample

228 megafaunal communities along the axis of the canyon at different “target” depths.

229 Some depth variation is expected given the geomorphology of submarine canyons:

230 walls are typically at shallower depths than the floor. We did not sub-sample

231 transects horizontally since the main feature of interest (the OMZ) is vertically

232 stratified, and this gradient occurs at a broader scale than the overlap in depth

233 range at the shallower transects. The depth variation within transects is much

234 smaller than the depth variation between transects, particularly at depths > 400

235 m. In the interpretation of our results, we focus mainly on differences in patterns

236 among shallow, intermediate and deep depths and less on individual transects.

237 To show bathymetric patterns in megafaunal abundance throughout the canyon

238 along the OMZ gradient, mean abundance along 1-km transects was calculated from all

239 usable frames by dividing the total number of individuals observed with the total surface

240 area analyzed. Diversity was calculated for each 1-km transect using diversity indices

241 [morphospecies richness (S), Pielou’s evenness (J'), and Shannon-Weaver’s diversity

242 index (H')] and individual-based rarefaction analysis. All individuals in each transect

243 were pooled, yielding a single assemblage per transect. As the diversity indices can be

244 affected by sampling effort, an individual-based rarefaction index was calculated for each

245 transect (Hurlbert 1971). This was calculated by randomly re-sampling individuals for a

246 given sample size to create an expected morphospecies richness. The expected richness

247 for a normalized sample size allows comparisons among transects with a different

248 number of individuals. Expected morphospecies richness was calculated at the second

249 lowest number of individuals ($n = 50$), as well as double this sample size ($n = 100$), to

250 exhibit changes in richness with a small and large normalized sample size. The 800-m

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transect was excluded from diversity analysis because too few individuals were observed (n = 51) to provide sufficient data to display patterns in expected richness.

Correlations between faunal composition and environmental variables were investigated using a redundancy canonical analysis (RDA) which combines aspects of ordination and regression. Environmental factors included depth, concentration of dissolved oxygen and temperature averaged along the transect, as well as substrate type (pebbles vs soft sediment). Prior to analyses, **abundance was Hellinger-transformed to mitigate the weight given to species with low counts and 0 data**, while being appropriate in Euclidean method-based analyses (Legendre & Gallagher 2001). A forward selection of the environmental variables was first conducted to select a parsimonious model. The canonical relationship and the individual canonical axes were then tested using the maximum number of possible random permutations, given the relative number of variables and sites. Analyses were performed at the group and morphospecies levels.

All analyses were performed in the R environment using the ‘vegan’ package (Oksanen et al. 2015).

3. Results

3.1 Environmental data

Oxygen levels at the sea surface were approximately 5.0 ml L⁻¹, and decreased at the thermocline (~10 to 50 m depth) to ~ 2.0 ml L⁻¹. The oxygen minimum zone (OMZ) was relatively consistent among transects, occurring at intermediate depths, and extending from ~530 to ~1450 m. Within the OMZ, oxygen concentration declined to a minimum of 0.159 ml L⁻¹ at a depth of approximately 900 m (Fig. 2). **Variability in**

274 oxygen concentration and temperature values were minimal within transects. For
275 example variation at 400, 600, and 2000 m (average $\pm$ SD) was minimal (respectively
276 oxygen: 1.03 ± 0.09 ml L⁻¹, 0.53 ± 0.1 ml L⁻¹, 1.03 ± 0.04 ml L⁻¹; temperature: $6.32 \pm$
277 0.28 °C, 5.2 ± 0.2 °C, 2.1 ± 0.8 °C).

278 Substrate varied across depths from pebble-dominated sediment in the shallow
279 transects (200 to 400 m) to soft muddy sediment in the intermediate to deep transects
280 (600 to 2000 m) (Table 3; Fig. 3). At 200 m, cobbles and boulders were common, but
281 became increasingly rare with depth and were rarely seen at depths below 400 m. At
282 depths > 600 m, the substrate was mostly fine to very fine grain sediment (i.e. clay) and
283 was easily disturbed. Bioturbation, mainly tracks, but also burrows and sediment
284 displacement by fish, was common in the deeper transects, in particular within the OMZ
285 core (600- and 800-m transects).

286 3.2 Abundance and community composition

287 Epibenthic megafaunal distribution appeared related to depth and oxygen
288 concentration for most taxonomic groups (Fig. 4). Echinoidea were only present in the
289 shallower depths (200 to 400 m), whereas Porifera, Gastropoda, and Crinoidea extended
290 into the mid depths of the canyon (200 to 800 m). Pennatulacea and hydrozoans were
291 absent from the hypoxic transects (600 and 800 m), although they were present shallower
292 and deeper (Fig. 4). Alcyonacea were only present in the deepest transect (2000 m).
293 Actinaria, Decapoda, Holothuroidea, and Asteroidea were present throughout the canyon.

294 At a lower taxonomic level, all groups exhibited depth- and/or oxygen-related
295 distribution patterns. Three taxonomic groups only included a single morphospecies (i.e.
296 Crinoidea, Echinoidea and Gastropoda), while other groups included multiple

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297 morphospecies with different depth distributions (Table A.1). For example, 2 large
298 species of decapods (*Munida* sp. and *Pandalus platyceros*) were present at 200 and 300
299 m, whereas only a small decapod (Family Pandalidae) was present at the deeper transects.
300 Similarly for Holothuroidea, *Parastichopus leukothele* was only present at 200 to 400 m,
301 whereas different taxa were present at depths > 800 m (Table A.1). For Pennatulacea,
302 *Sessiflorae* sp. 1 was present at 200, 300, 400, and 2000 m, while a different
303 morhospecies, *Sessiflorae* sp. 2, was only present at 1500 and 2000 m.

304 Redundancy analysis (RDA) showed that, after forward selection, assemblages
305 (based on taxonomic groups) were significantly correlated to depth, temperature and,
306 marginally, to the presence of pebbles ($R^2_{adj} = 0.49$, $p = 0.007$, Fig. 5). Only the first
307 canonical axis was significant and explained 45.2% of the total variation in abundance (p
308 = 0.04). This axis separated the warmer shallow sites (from 200 to 600 m) from the deep
309 colder ones (1500 and 2000 m). The presence of Porifera, hydrozoans and echinoids
310 characterized the shallow rocky (i.e. pebbles) sites, while ophiuroids and pennatulaceans
311 were associated with the deep site. Even though neither the second axis nor the oxygen
312 concentration explained a significant amount of the variation in the assemblages, it is
313 noteworthy that the second canonical axis actually separated oxygenated sites from those
314 located inside the OMZ (i.e. 600 and 800 m). Additional samples within the OMZ and
315 outside of the OMZ at similar depths are needed to verify and test this pattern. Similar
316 patterns were observed in analyses using morphospecies, but the canonical relationship
317 was weaker with the model explaining only 29% of the total variance. However, results
318 using morphospecies must be treated with caution as the species matrix was zero-inflated
319 (75% of data).

3.3 Faunal patterns across the submarine canyon

At the shallower depths of Barkley Canyon (200 to 600 m), bathymetry varied along each 1-km transect across the width of the canyon (Fig. 6). Some taxonomic groups exhibited distributions related to the cross-canyon geomorphology of the seafloor along these transects. Porifera were found on the walls of the canyon at all 4 depths (Fig. 6). At 200, 300, and 400 m, in particular, abundance was greater along the northwest wall than the southeast wall of the canyon (Fig. 6). At 600 m, Porifera were only present on the southeast wall. In contrast, echinoids were present mainly at the axis of the canyon, particularly at 200 and 300 m (Fig. 6). *Munida* sp. and *P. platyceros* were present along the northwest wall at 200 m. At 300 m, *Munida* sp. and Family Pandalidae were present along the northwest wall, but at 600 m, Family Pandalidae was present throughout the transect (albeit at a much lower abundance), while the *Munida* sp. and *P. platyceros* were absent (Fig. 6).

3.4 Patterns in diversity

The greatest megafaunal richness was recorded at 300 m and 2000 m and the lowest at 400 m and 800 m (Fig. 7b). Richness ranged from 9 morphospecies at 800 m to 16 morphospecies at 2000 m, but showed no bathymetric trend (Fig. 7b). Similarly, there was no clear bathymetric pattern in the Shannon-Weaver diversity index or Pielou's evenness but transects with the lowest diversity (200 m and 1500 m) also showed the lowest evenness (Fig. 7c). Expected richness showed a bimodal trend with richness peaking at 300 and 2000 m (Fig. 7d).

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341 3.5 *Species aggregations in response to macrodetritus*

342 Drift kelp was found along 3 transects at 200, 300, and 1500 m depth, with the

343 largest piece at 300 m (Table 4). At 200 m, echinoids aggregated on the drift kelp, with 3

344 individuals found on the kelp itself (Fig. 8), while at 300 m, larger aggregations (20 to 30

345 individuals) were observed (Fig. 8). At 1500 m, there were no aggregations of mobile

346 megafauna on the kelp, however, ophiuroids and holothuroids were present in high

347 abundances along the 40-m transects (Fig. 8). Echinoidea aggregated at 200 and 300 m,

348 but were not present at the deeper 1500-m transects. Although not targeted during

349 sampling, an aggregation of the gastropod *Fusitriton oregonensis* of 34 individuals m⁻²

350 was also observed on a carcass of a fish at 174 m depth (Fig. 9).

4. Discussion

4.1 Bathymetric zonation in abundance

Megafauna show distinct zonation along the upper, mid, and lower **canyon**. The redundancy canonical analysis (RDA) indicated that the abundance of taxonomic groups was significantly correlated with depth, temperature and the presence of pebbles. **However, because both temperature and the presence of pebbles varied with depth, the individual effects of each factor are confounded.** Porifera, hydrozoan, and echinoids were associated with the shallow rocky sites (200-600 m). Crinoids and gastropods were also found only within the shallow-mid region of the canyon. Porifera and crinoids are both filter feeders and require strong flow to obtain nutrients and hard substrata for attachment (Vogel 1977). The substrate composition (coarse grain sediment: pebbles, cobbles, and boulders) indicates that flow was higher in the shallower region of the canyon. Alternatively, disturbances, such as sediment slumps and turbidity currents, which can be common in canyons, may also restrict the distribution of sessile filter feeders (Inman et al. 1976; Vetter et al. 2010; reviewed in Puig et al. 2014). In Gioia canyon, Pierdomenico et al. (2016) found that the highly active canyon head (turbidity flows and high sedimentation) was relatively devoid of megafauna except for a robust species of sea pens.

Some species were only found at the shallow and mid depths of the canyon. The gastropod *Fusitriton oregonesis* has been recorded from the intertidal zone to 2300 m (Smith 1970). However, in our study, this species was only found in the mid-canyon including the OMZ, but not deeper, indicating that factors other than depth or oxygen, **such as presence of food or larvae distribution,** may be limiting its distribution. *F. oregonesis* is a carnivore feeding on other mollusks, but we observed aggregations

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375 **on fish carcasses. It is thus possible that it could be exploiting food sources**
376 **concentrated within the narrow margins of the canyon.** The echinoid
377 *Stronglocentrotus fragilis* was found only at shallow depths < 400 m, above the OMZ,
378 despite unpublished records of occurrence at 800 m within Barkley Canyon (Chauvet,
379 unpublished data). *S. fragilis* has a depth distribution from 30 m to > 2000 m (Schultz).
380 However, depths below the OMZ fall outside those where they are most abundant (0-600
381 m) (Duffy et al. 2014; Schultz 2015). **In addition, along the Southern Californian**
382 **Bright, *S. fragilis* have experienced a habitat expansion into shallower slope waters**
383 **from deep-water environments with increased densities along the upper continental**
384 **shelf (above 500 m) between 2003-2013 (Sato et al. 2017) indicating that *S. fragilis***
385 **may become increasingly more common in shallower shelf waters, such as Barkley**
386 **Canyon. Alternatively *S. fragilis* could be exploiting drift kelp funneled and**
387 **deposited in the shallow canyon.** Ophiuroids and pennatulids were associated with the
388 deep-water habitats (1500-2000 m), likely because of an **avoidance of low oxygen.**

389 In contrast, some groups were present throughout most of the canyon, although
390 different morphospecies occurred at different depths. For example, of the holothuroid
391 species that were identified, *Parastichopus leukothele* was present in the shallow
392 transects (200-, 300-, 400-m) and *Pannychia moseleyi* and *Scotoplanes theeli* were found
393 in deeper (>800-m) transects, reflecting previously recorded bathymetric patterns (Maluf
394 1987; Blaine 2011). *P. leukothele* has been found in both soft and hard sediment areas but
395 rarely deeper than 300 m in Californian waters (Blaine 2011), likely indicating that depth
396 **restricts their distribution.** Deep-water holothuroids (such as *P. moseleyi* and *S. theeli*)
397 have tentacle structures specially designed to exploit deep-water detritus (Carney 2005)

and may be better suited to foraging in deep waters. *P. moseleyi* has been observed aggregating and feeding on such detrital patches in canyons in California as shallow as 300 m (Vetter & Dayton 1999). The shift in decapod abundance **with increasing depth** from two larger species to a smaller one (Family *Pandalidae*) may reflect a decrease in size associated with a decrease in available energy (Rex et al. 2006) or a response to low-oxygen conditions, discussed below. Actiniaria and asteroids were also present throughout the canyon, but identification at higher taxonomic resolution revealed a species-specific pattern in zonation. Order Actiniaria contains species with many different modes of substrate attachment, on either hard or soft sediments or both (Ammons & Daly 2008). The transition from pebble-dominated to soft sediments could restrict some of the species from recruiting in deeper waters. While present at all depths, few actinarian species found in this study appear in multiple transects (except *Actinauge verrillii*, Actiniaria sp. 5, and Actiniaria sp. 7) **indicating that substrate alone does not regulate distribution, and other factors, such as temperature, food availability, species-specific patterns, or patterns in recruitment may play a role since they may also vary at the different depths in the canyon.**

4.2 Zonation in abundance relative to the OMZ

While statistical analyses did not reveal a significant pattern, the presence of the OMZ appeared to restrict the distribution and abundance of some taxa. The absence of a significant correlation could be due to the small number of transects (and thus reduced statistical power) in the OMZ. Benthic fauna found within OMZs have been reported as primarily composed of protozoan and metazoan meiofauna, **likely because small size allows for a lower oxygen requirement and aerobic adaptations for more effective**

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422 **oxygen uptake**, whereas megafauna are rare or absent (Childress & Siebel 1998; Levin
423 2003; Callow et al. 2014). In Barkley Canyon, a size-related distribution was observed
424 for decapods. The large species spot prawn *Pandalus platyceros* - known to only occur in
425 oxic conditions and living as deep as 400 m (Butler 1964; Matabos et al. 2012) - was
426 absent below 200 m and replaced by smaller species. Pennatulids, hydrozoans, and
427 echinoids were absent within the OMZ, indicating that these taxa may have a
428 physiological lack of tolerance, or a lower threshold, to oxygen levels below 0.05 ml L⁻¹.
429 Echinoderms were nonetheless reported to be the most tolerant to hypoxic events
430 (Vaquer-Sunyer & Duarte 2010). However, substrate also changed from pebbles at
431 shallow depths to soft clay-like sediment at the upper boundary of the OMZ (600 m).
432 Although depth and terrain steepness contribute to megafaunal distribution, substrate can
433 be the main regulatory factor in some canyons.

434 Although changes in oxygen and substrate are confounded in Barkley Canyon, it
435 appears that the change in substrate may regulate the abundance of hydrozoans, while
436 low oxygen may limit pennatulids. The same morphospecies of Pennatulacea was found
437 both above and below the OMZ in pebble-dominated and soft sediment, but not within
438 the OMZ. In contrast, different hydrozoan morphospecies were found above and below
439 the OMZ indicating that either sediment or oxygen may be regulating their patterns in
440 abundance. Duffy et al. (2014) also were unable to disentangle the effects of depth and
441 oxygen on species distribution in submarine canyons in a weak OMZ off the coast of
442 California. Squat lobsters were only found in the shallow, well oxygenated transect (200
443 m), which is consistent with a study in the Gulf of California that found that most *Munida*
444 species (8 of 9 studied) were distributed in shallow waters above the OMZ and

experienced a physiological oxygen threshold at 0.10 ml L^{-1} (Hendrickx & Serrano 2013). However, *Munida quadrispina* is also highly tolerant to severe hypoxia (Matabos et al. 2012), indicating that improved species identification could help better understand species distribution.

In our study, some taxa were not restricted by low-oxygen conditions, such as gastropods, which were present in the core of the OMZ. Gastropods are known to have a higher tolerance to hypoxic conditions and can capitalize on the organic matter preserved in the low O_2 environment (Cowie & Hedges, 1992; Levin, 2003; Vaquer-Sunyer & Duarte, 2008). However, **even taxa expected to be susceptible to hypoxic conditions (Levin 2003) were present in the OMZ in this study, such as decapods** (Family Pandalidae) and echinoderms (asteroidea including *Crossaster borealis*, *Pannychia moseleyi*, and actiniaria species).

Overall, there was no evidence that megafauna abundance were significantly reduced in the OMZ in Barkley Canyon. Oxygen may not be the regulating factor in this habitat; rather the increase in habitat heterogeneity or funneled food may allow low-oxygen tolerant taxa to survive in the OMZ. However, further study of this OMZ may provide more information on this OMZ-submarine canyon dynamics.

Many studies suggest the presence of “edge effects” as an increase in biomass at the edge of severely hypoxic areas due to combined release of oxygen and a supply of organic material in the sediment (Levin 2003; Levin & Sibuet 2012). Species in OMZ also benefit from a release in predation (Levin 2003). In our study, edge effects were apparent for ophiuroids with abundance being highest at 1500 m. At that depth, oxygen concentration was above 0.5 ml L^{-1} and total organic carbon was highest in the canyon

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(Neus Campanya I. Llovet unpublished data). The presence of “edge effects” for this taxon is consistent with a study along the California continental margin, where ophiuroids had the highest biomass along the lower OMZ boundary (Thompson et al. 1985).

4.3 Patterns in diversity

Globally, diversity exhibits a parabolic shape peaking between 1500 and 2500 m (Menot et al. 2010). Submarine canyons can exhibit higher biodiversity than the continental margin at corresponding depths (Vetter & Dayton 1999; De Leo et al. 2010; McClain & Barry 2010; Vetter et al. 2010). However, diversity can be depressed within OMZs along continental margins (Levin 2003; Gooday et al. 2010) .

In Barkley Canyon, diversity (measured with indices) and expected richness exhibited a bimodal distribution, with a depressed expected richness within the OMZ, and peaking at 300 and 2000 m. The pattern may reflect the combined effects on diversity of depth (peaking at 2000 m) and low oxygen (depressed between 400 and 2000 m). De Leo et al. (2016) recorded 46 species of megafauna from video transects on the Northeastern Pacific continental margin over similar depths as in our study, but outside the OMZ (30.8-km transect from 300 to 1300 m) compared to 55 species recorded inside the canyon in this study (despite a relatively greater sampling effort in De Leo et al. 2016). This increase in species richness is consistent with the hypothesis that submarine canyons, despite the presence of the OMZ, can exhibit higher megafaunal diversity than similar depths along the continental margin.

4.4 Horizontal patterns in abundance across the canyon

Because the 1-km transects were done perpendicularly to the canyon axis, the ones at shallow target depths covered a range of geomorphologies, from the relative flat axis to the steep walls towards the NW and SE boundaries of the canyon.

Patterns in megafaunal abundance were related to seafloor geomorphology however, these patterns may also be confounded with depth. Nonetheless, poriferans were more abundant on the NW wall rather than on the SE wall of Barkley Canyon, possibly indicating a more suitable habitat with increased bottom current flow or breaking internal waves and the presence of suspended organic material (Klitgaard & Tendal 2004; Beazley et al. 2015). Canyons have dynamic flows, including upwelling, downwelling, internal tides, and asymmetrical currents that could provide enhanced flow to one side of the canyon or enhanced organic re-suspension (Allen et al. 2001; Allen & Durrieu de Madron 2009). Similarly, in Whittard Canyon in the NE Atlantic, megafaunal abundance was enhanced on the eastern relative to the western canyon due to environmental heterogeneity (Amaro et al. 2016). In contrast, the higher abundance of *Strongylocentrotus fragilis* along the axis than the walls of Barkley Canyon (200-400 m) may indicate an increase in food availability in a depositional region. In Carmel Canyon, along the Californian continental margin, the biomass of detritus kelp was significantly higher along the axis of the canyon than on the canyon walls (Harrold et al. 1998).

4.5 Species aggregations in response to macrodetritus

Submarine canyons are conduits for organic detrital material and sediment from the shelf to the deep sea, acting as a food source and causing megafaunal aggregations (Vetter 1994; Harrold et al. 1998; Vetter & Dayton 1999; Puig et al. 2014). Drift kelp in

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512 Barkley Canyon was surveyed to investigate abundance patterns at fine spatial scales.

513 Opportunistic mobile epifauna such as echinoids, holothuroids, and ophiuroids would be

514 expected to aggregate on food sources. The sea urchin *Strongylocentrotus fragilis*

515 aggregated on detrital kelp at 200 and 300 m, but not at 1500 m, which falls outside its

516 bathymetric distribution (Schultz 2015). The holothurian *Pannychia moseleyi* is also

517 known to aggregate on detrital plant material (Vetter & Dayton 1999), but was not

518 present near the kelp. The holothurians that were present did not aggregate near the kelp

519 and likely do not feed on kelp but on particulate organic carbon. Typically, the deep sea

520 has a low but predictable rate of food supply from sinking surface primary production

521 (Gage & Tyler 1991) and faunal biomass declines with depth because of this low organic

522 input (Carney 2005; Rex et al. 2006). The presence of organic detritus (either drift kelp or

523 fish falls) provides a food source, **in addition to organic material funneled from the**

524 **shelf, and could explain the increased biomass typically found at fine scales within**

525 **submarine canyons when compared to similar depths in non-canyon habitats** (De

526 Leo et al. 2010; Harrold et al. 1998).

527 **5. Conclusions**

528 In Barkley Canyon, British Columbia, faunal zonation appears to be influenced by

529 the combination of depth, oxygen and substrate. Although total megafaunal abundance

530 did not decrease with oxygen, expected richness and diversity did. Comparisons with

531 patterns from other canyons can be difficult because variability can be high, even

532 between canyons in close proximity or within a single canyon (Huvenne & Davis 2014;

533 Van Oevelen et al. 2011). Our study only focused on epibenthic megafauna and each

534 transect covered an average surface area of ~120 m².

Continental margins, such as the Canadian Pacific margin, are facing anthropogenic threats, as human exploitation expands from shallow margins into the deep sea (Ramirez-Llodra et al. 2011; Levin & Sibuet 2012). In addition, oxygen minimum zones are predicted to increase in size due to increasing sea surface temperature and increased ocean stratification, particularly in the North Pacific Ocean, and could result in a global decrease in diversity (Helly & Levin 2004; Bograd et al. 2008; Chan et al. 2008; Diaz & Rosenberg 2008; Falkowski et al. 2011). This study adds insight into species distribution and the possible mechanisms underlying these patterns. Considering the increasing anthropogenic and hypoxic threats and the importance of continental margin and submarine canyons, understanding faunal patterns and ecosystems are essential for the Northeast Pacific margin environmental management.

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For Peer Review

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Figure captions

Figure 1. Bathymetric map of Barkley Canyon a submarine canyon off the western coast of Vancouver Island, British Columbia, Canada. Diamonds indicate the location of 1-km transects along isobaths within the canyon (target depths: 200, 300, 400, 600, 800, 1500, 2000 m).

Figure 2. Oxygen, salinity, and temperature profiles measured during the ROPOS dive to 2000 m in Barkley Canyon, British Columbia, Canada in September 2013. The red dashed line indicates the threshold oxygen concentration between oxic and Oxygen Minimum Zone conditions ($< 0.5 \text{ ml L}^{-1}$, Levin 2003).

Figure 3. Substrate at different depths within Barkley Canyon, British Columbia, Canada, in September 2013 (A=176 m, B=213 m, C=321 m, D=578 m, E=768 m, F=1489 m). Images D and E occur within the OMZ. The scale bar is 10-cm.

Figure 4. Mean abundance (logarithmic scale) of the dominant taxonomic groups present at 7 depths in Barkley Canyon, British Columbia, Canada in September 2013. Absence of taxa is indicated in white. Transects at 600 and 800 m are within the oxygen minimum zone ($< 0.5 \text{ ml L}^{-1}$).

Figure 5. Redundancy canonical analysis of environmental factors (depth, temperature, substrate, and oxygen concentrations) and megafaunal abundance at the group level. The first axis (RDA 1) accounts for 45.2% of the total variation in the data.

Figure 6. Abundance (individuals m^{-2}) of three taxonomic groups (Porifera, Echinoidea, Decapoda) binned into 50-m distances along 1-km transects at four target depths (200, 300, 400, and 600 m) in Barkley Canyon, British Columbia, Canada, in September 2013 (square-root scale shown for Decapoda only). NW and SE, respectively, represent the northwest and southeast walls of the canyon. The total number of individuals sampled at each depth is indicated. Decapoda were composed of three different morphologically different taxa. A second poriferan morphospecies was removed because of low sample size ($n=1$).

Figure 7. Megafaunal abundance and diversity at 7 transect depths (200, 300, 400, 600, 800, 1500, 2000 m) in Barkley Canyon, British Columbia, Canada in September 2013. (A) Megafaunal abundance (B) morphospecies richness, (C) diversity indices, (D) expected morphospecies richness ($\pm$ standard errors) for 50 and 100 individuals. * Expected richness cannot be estimated for a sample size of 100 individuals since too few individuals were recorded at 400 m ($n=86$) and 800 m ($n=51$).

Figure 8. Abundance (individuals) of Echinoidea, Holothuroidea, and Ophiuroidea present along 40-m cross transects over drift kelp located at the centre of the transect, at 3 depths in Barkley Canyon (200 m, 300 m, and 1500 m).

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768 **Figure 9.** Aggregation of the Oregon hairy triton *Fusitriton oregonensis* on a carcass of
769 an unidentified large fish (surface area=396.9 cm²) at 174 m, in Barkley Canyon.

For Peer Review

Table 1. Data collected over 7 1-km transects along isobaths in Barkley Canyon, British Columbia, Canada with the ROV ROPOS in September 2013. Target depth and start position for each transect are indicated.

Dive	Target depth (m)	Date (YY-MM-DD)	Depth range (m)	Length (m)	Average distance between frames (m) [± SD]	# Total frames	# Usable frames	Total surface area surveyed (m ²)	Longitude	Latitude
R1654	200	2013-09-14	168-200	992	8 [±2]	131	125	123.9	125° 53' 8" W	48° 23' 49" N
R1655	300	2013-09-15	183-306	986	7 [±2]	152	132	134.3	125° 53' 51" W	48° 23' 46" N
R1655	400	2013-09-15	268-394	928	8 [±2]	123	105	105.8	125° 54' 40" W	48° 24' 16" N
R1658	600	2013-09-16	497-626	1002	7 [±2]	152	102	92.0	125° 56' 36" W	48° 22' 46" N
R1657	800	2013-09-16	635-801	988	8 [±5]	142	125	126.1	125° 59' 7" W	48° 20' 42" N
R1656	1500	2013-09-15	1479-1511	1006	8 [±2]	136	136	136.3	126° 9' 47" W	48° 15' 5" N
R1653	2000	2013-09-12	1863-2001	1004	7 [±2]	135	135	135.4	126° 19' 35" W	48° 7' 40" N

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Table 2. Data collected over cross transects in Barkley Canyon opportunistically performed upon encounter with drift kelp. The cross transects were centered over the drift kelp (position at kelp is indicated).

Dive	Target depth (m)	Date (YY-MM-DD)	Kelp depth (m)	Length of each segment (m)	Kelp Longitude	Kelp Latitude
R1654	200	2013-09-14	169	69, 86	125° 53' 19" W	48° 24' 21" N
R1655	300	2013-09-15	313	44, 38	125° 54' 39" W	48° 24' 15" N
R1656	1500	2013-09-15	1509	47, 39	126° 10' 14" W	48° 15' 28" N

Table 3. Qualitative description of the substrate at each 1-km transect in Barkley Canyon.

Dive	Depth (m)	Qualitative description of substrate
R1654	200	Pebbles and shell debris throughout the transect with regular occurrence of cobbles and large boulders
R1655	300	Large cobbles and boulders present on the edges of the transect; mid transect characterized with soft fine sediment with pebbles and cobbles
R1655	400	Fine sediment with pebbles and occasional cobbles, boulders rare
R1658	600	Soft muddy sediment, high level of bioturbation, and easily disturbed
R1657	800	Soft muddy clay-like sediment, very easily disturbed, very few pebbles or shell hash
R1656	1500	Soft muddy sediment with burrows and bioturbation
R1653	2000	

Table 4. Depth, weight, and size of drift kelp sampled from the cross transects.

Dive	Sample depth (m)	Frozen Weight (g)	Longest blade length (cm)	Observations
R1654	169	84.33	N/A	Fragmented
R1655	313	1725.1	158	Full kelp with stipe and blades
R1656	1509	29.13	N/A	Fragmented

Appendix A:

Table A.1. Mean ($\pm$ SD, for n see Table A.2) density (ind. 100 m⁻²) of morphospecies along the 7 1-km transects in Barkley Canyon. Morphospecies that could be differentiated by morphological features but not be identified are depicted by sp. (species) number.

Taxa	Average Density (ind. 100 m ⁻²)						
	200 m	300 m	400 m	600 m	800 m	1500 m	2000 m
Asteroidea							
<i>Orthasterias koehleri</i>	0.8	0.8	0.9				
Genus <i>Psuedarchaster</i>	1.7						
<i>Cheiraster dawsoni</i>		0.8					
<i>Pteraster</i> sp. 1		1.5					
<i>Ctenodiscus</i> sp.		0.8		1			1.5
Genus <i>Henricia</i>			0.9				
<i>Solaster borealis</i>				1	4.8		
Asteroidea sp. 1					0.8		
<i>Pteraster</i> sp. 2					0.8	0.7	
Genus <i>Hymenodiscus</i>						0.7	
Asteroidea sp. 2						0.7	
Asteroidea sp. 3							3
Asteroidea sp. 4							0.7
Holothuroidea							
<i>Parastichopus leukothele</i>	2.5	2.2	3.8				
<i>Pannychia moseleyi</i>					1.6		
<i>Scoloplanes theeli</i>						29.3	1.5
<i>Elasipodida</i> sp. 1							5.9
Pennatulacea							
Sessiflorae sp. 1	1.8	0.7	1.2				48
Sessiflorae sp. 2						9.5	
Alyconacea							
Alyconacea sp. 1							5.9
Alyconacea sp. 2							3
Crinoidea							
<i>Comatulida</i> sp. 1		3.7	1.9	4	3.2		
Porifera							
Porifera sp. 1	7.5	6	54.8	89.9	0.8		
Porifera sp. 2	0.8						
Echinoidea							
<i>Strongylocentrus fragilis</i>	36.3	27.2	13.3				
Gastropoda							
<i>Fusitriton oregonensis</i>	2.4	1.5		18	3.2		

Decapoda						
<i>Munida</i> sp.	347.4	16				
<i>Pandalus platyceros</i>	1.7					
Family Pandalidae		4.7	37.6	22.2	4.4	5.9
Hydrozoa						
Hydrozoa sp. 1		26.8	1.9			
Hydrozoa sp. 2						0.7
Ophiuroidea						
Ophiurida sp. 1		0.9	6.1			
<i>Asteronyx</i> sp.					9.5	
Ophiurida sp. 2					295.7	48.8
Ophiurida sp. 3						3
Actiniaria						
Actiniaria sp. 1		3				
Actiniaria sp. 2		1.5				
Actiniaria sp. 3		3.8				
Actiniaria sp. 4			1.9			
Actiniaria sp. 5			1			3
<i>Actinauge verrillii</i>			4.9		1.5	
Actiniaria sp. 6			1.1			
Actiniaria sp. 7			28			0.7
Actiniaria sp. 8			1.2			
Actiniaria sp. 9				1.6		
Actiniaria sp. 10					2.2	
Actiniaria sp. 11					1.5	
Actiniaria sp. 12					7.3	
Actiniaria sp. 13						0.7
Actiniaria sp. 14						3.7

Table A.2. Standard deviation of mean density (ind. 100 m⁻²) of morphospecies along the 7 1-km transects in Barkley Canyon. Morphospecies that could be differentiated by morphological features but not be identified are depicted by sp. (species) number.

Taxa	Standard Deviation (ind. 100m ⁻²)						
	200 m	300 m	400 m	600 m	800 m	1500 m	2000 m
Asteroidea							
<i>Orthasterias koehleri</i>	8.9	8.7	9.7				
Genus <i>Psuedarchaster</i>	13.8						
<i>Cheiraster dawsoni</i>		8.7					
<i>Pteraster</i> sp. 1		8.7					
<i>Ctenodiscus</i> sp.		8.7		1.3			12.1
Genus <i>Henricia</i>			9.7				
<i>Crossaster borealis</i>				1.3	25		
Asteroidea sp. 1					8.8		
<i>Pteraster</i> sp. 2					8.9	8.5	
Genus <i>Hymenodiscus</i>						8.6	
Asteroidea sp. 2						8.6	
Asteroidea sp. 3							12.1
Asteroidea sp. 4							8.6
Holothuroidea							
<i>Parastichopus leukothele</i>	16.2	14.8	19.1				
<i>Pannychia moseleyi</i>					12.5		
<i>Scoloplanes theeli</i>						62.1	12.1
<i>Elasipodida</i> sp. 1							23.6
Pennatulacea							
<i>Sessiflorae</i> sp. 1	14.5	8.6	12.9				76.9
<i>Sessiflorae</i> sp. 2						31.9	
Alyconacea							
Alyconacea sp. 1							26.6
Alyconacea sp. 2							17
Crinoidea							
<i>Comatulida</i> sp. 1		22.6	13.7	24.1	28.3		
Porifera							
Porifera sp. 1	137.9	15.8	129.3	389.5	8.9		
Porifera sp. 2	9.5						
Echinoidea							
<i>Strongylocentrus fragilis</i>	93.1	68.7	5.1				
Gastropoda							
<i>Fusitriton oregonensis</i>	15.3	12.1		51.9	17.6		
Decapoda							
<i>Munida</i> sp.	624	83.6					

<i>Pandalus platyceros</i>	13.8					
Family Pandalidae	4.6	81.7	53.4	2.6	23.6	
Hydrozoa						
Hydrozoa sp. 1	134.5	13.7				
Hydrozoa sp. 2						8.6
Ophiuroidea						
Ophiurida sp. 1		9.7	52.3			
Asteronyx sp.				36.2		
Ophiurida sp. 2				242.5		72
Ophiurida sp. 3						17
Actiniaria						
Actiniaria sp. 1	21.2					
Actiniaria sp. 2	12.2					
Actiniaria sp. 3	19.1					
Actiniaria sp. 4		13.7				
Actiniaria sp. 5		9.7				17
<i>Actinauge verrillii</i>			25.8	12		
Actiniaria sp. 6			11.1			
Actiniaria sp. 7			73.5			8.6
Actiniaria sp. 8			11.7			
Actiniaria sp. 9				12.6		
Actiniaria sp. 10					25.7	
Actiniaria sp. 11					12	
Actiniaria sp. 12					28.8	
Actiniaria sp. 13						8.6
Actiniaria sp. 14						18.9

Bathymetric map of Barkley Canyon a submarine canyon off the western coast of Vancouver Island, British Columbia, Canada. Diamonds indicate the location of 1-km transects along isobaths within the canyon (target depths: 200, 300, 400, 600, 800, 1500, 2000 m).

150x110mm (300 x 300 DPI)

Oxygen, salinity, and temperature profiles measured during the ROPOS dive to 2000 m in Barkley Canyon, British Columbia, Canada in September 2013. The red dashed line indicates the threshold oxygen concentration between oxic and Oxygen Minimum Zone conditions (< 0.5 ml L⁻¹, Levin 2003).

50x70mm (300 x 300 DPI)

Substrate at different depths within Barkley Canyon, British Columbia, Canada, in September 2013 (A=176 m, B=213 m, C=321 m, D=578 m, E=768 m, F=1489 m). Images D and E occur within the OMZ. The scale bar is 10-cm.

112x148mm (300 x 300 DPI)

Mean abundance (logarithmic scale) of the dominant taxonomic groups present at 7 depths in Barkley Canyon, British Columbia, Canada in September 2013. Absence of taxa is indicated in white. Transects at 600 and 800 m are within the oxygen minimum zone (< 0.5 ml L⁻¹).

102x92mm (300 x 300 DPI)

Redundancy canonical analysis of environmental factors (depth, temperature, substrate, and oxygen concentrations) and megafaunal abundance at the group level. The first axis (RDA 1) accounts for 45.2% of the total variation in the data.

92x47mm (300 x 300 DPI)

Abundance (individuals m⁻²) of three taxonomic groups (Porifera, Echinoidea, Decapoda) binned into 50-m distances along 1-km transects at four target depths (200, 300, 400, and 600 m) in Barkley Canyon, British Columbia, Canada, in September 2013 (square-root scale shown for Decapoda only). NW and SE, respectively, represent the northwest and southeast walls of the canyon. The total number of individuals sampled at each depth is indicated. Decapoda were composed of three different morphologically different taxa. A second poriferan morphospecies was removed because of low sample size (n=1).

160x116mm (300 x 300 DPI)

Megafaunal abundance and diversity at 7 transect depths (200, 300, 400, 600, 800, 1500, 2000 m) in Barkley Canyon, British Columbia, Canada in September 2013. (A) Megafaunal abundance (B) morphospecies richness, (C) diversity indices, (D) expected morphospecies richness ($\pm$ standard errors) for 50 and 100 individuals.

* Expected richness cannot be estimated for a sample size of 100 individuals since too few individuals were recorded at 400 m (n=86) and 800 m (n=51).

199x122mm (300 x 300 DPI)

Abundance (individuals) of Echinoidea, Holothuroidea, and Ophiuroidea present along 40-m cross transects over drift kelp located at the centre of the transect, at 3 depths in Barkley Canyon (200 m, 300 m, and 1500 m).

107x143mm (300 x 300 DPI)

Aggregation of the Oregon hairy triton *Fusitriton oregonensis* on a carcass of an unidentified large fish (surface area=396.9 cm²) at 174 m, in Barkley Canyon.

62x62mm (300 x 300 DPI)