

1 Changes in deep-water epibenthic megafaunal assemblages in relation to seabed slope  
2 on the Nigerian margin

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13  
14  
15 Abstract

16  
17 Local-scale habitat heterogeneity associated with changes in slope is a ubiquitous  
18 feature of bathyal continental margins. The response of deep-sea species to high  
19 habitat heterogeneity is poorly known and slope can be used as a proxy for many  
20 important ecological variables, such as current flow, sedimentation and substratum  
21 type. This study determines how slope angle effects megafaunal species density and  
22 diversity at the Usan field, offshore Nigeria, between 740-760 m depth. This deep-  
23 water area is increasingly exploited for hydrocarbons, yet lacking in baseline  
24 biological information. Replicated remotely operated vehicle video transect surveys  
25 were carried out using industry infrastructure (through the SERPENT Project) at a  
26 representative range of slopes (1°, 3°, 11° and 29°). Twenty-four species of benthic  
27 megafaunal invertebrate were found, numerically dominated by the echinoid  
28 *Phormosoma placenta*, and nine species of fish were observed. Megafaunal  
29 invertebrate deposit feeder density decreased significantly with increasing slope  
30 (density range 0.503 - 0.081 individuals m<sup>-2</sup>). Densities of megafaunal suspension  
31 feeders were very low except at the highest slope site (mean density 0.17 m<sup>-2</sup>). Overall  
32 species richness was greater on steeper slopes, although the richness of deposit  
33 feeders was not affected. Reduced labile organic matter in sediments on steeper slopes

34 likely reduced deposit feeder densities, but increased current flow at higher slopes  
35 allowed both increased richness and density of suspension feeders.

36

37 Keywords:

38 Deep-sea; slope; habitat heterogeneity; landscape; Phormosoma placenta; Gulf of  
39 Guinea, Nigeria; video

40

41

42 1. Introduction

43

44

45 Habitat heterogeneity at local scales is a ubiquitous feature of bathyal continental  
46 margins and exerts a fundamental influence on the diversity and structure of benthic  
47 communities (Levin and Dayton, 2009). The ‘habitat heterogeneity hypothesis’ is one  
48 of the cornerstones of ecology (e.g. MacArthur and Wilson, 1967; Simpson, 1949). It  
49 assumes that structurally complex habitats may provide more niches and diverse ways  
50 of exploiting the environmental resources and thus increase species diversity (Tews *et*  
51 *al.*, 2004). Characterisation of the seabed in terms of terrain parameters, such as slope  
52 and aspect, is a potentially valuable tool for classifying the structural complexity of  
53 the seabed and delineating regions of seabed that may support particular fauna and  
54 therefore provide a distinct habitat (Wilson *et al.*, 2007). These techniques, broadly  
55 classified as habitat mapping, have been successful in shallow waters (Lundblad *et*  
56 *al.*, 2006) and are receiving increased attention in deep water (Jones and Brewer,  
57 2012; Wilson *et al.*, 2007). Slope is a commonly used and important parameter in  
58 these analyses, but direct assessment of changes in deep-water assemblages in relation  
59 to seabed slope have not (to the author’s knowledge) been assessed quantitatively.  
60 Flat areas tend to exhibit different seabed facies and support communities that are  
61 different to those inhabiting steeply sloping areas (Lundblad *et al.*, 2006; Schlacher *et*  
62 *al.*, 2007). Slope, as with depth, is not a direct environmental factor that controls  
63 biological communities; rather it is a useful proxy for correlated but unmeasured  
64 factors. In the case of slope, these environmental factors range across the scale of  
65 investigation but include a complex of environmental variables, primarily habitat  
66 heterogeneity (Schaff *et al.*, 1992), local current flow (Noble and Mullineaux, 1989;  
67 Palardy and Witman, 2011), sedimentation, substratum type, food availability and  
68 colonisation (Butman, 1990; Butman *et al.*, 1994; Gage, 1997). Shallow water

69 research suggests that these factors may lead to increases in density (Sebens, 1985),  
70 higher diversity (Palardy and Witman, 2011), elevated growth rates and changes in  
71 species distribution (Leichter and Witman, 1997) as well as functional changes in  
72 benthic communities, for example favouring suspension feeding over deposit feeding  
73 organisms (Jumars and Nowell, 1984). It is important to assess the role of slope-  
74 related factors in driving the structure of deep-water benthic faunal assemblages  
75 (Levin *et al.*, 2001; Tyler, 1995), particularly in areas of high habitat complexity such  
76 as canyons (De Leo *et al.*, 2010; Rowe *et al.*, 1982) and seamounts (Clark *et al.*, 2010;  
77 Genin *et al.*, 1986).

78

79 By combining spatially-accurate quantitative seabed imaging techniques with high-  
80 resolution acoustic data on submarine topography and sediment properties fine-scale  
81 patterns in megafaunal biology can be linked to the broad-scale patterns in habitat  
82 type and subsea landscape (Baguley *et al.*, 2006; Wilson *et al.*, 2007). Given the sheer  
83 size and difficulties of accessing the deep-sea environment, accurate extrapolation of  
84 fine-scale observations using information on the important physical controls for  
85 faunal distribution is vital to describe the important broad-scale patterns in benthic  
86 biology (Sanchez *et al.*, 2008; Williams *et al.*, 2010). Characterising variation in  
87 biodiversity and biological assemblage structure in response to specific terrain  
88 parameters, such as slope, are important to help understand the underlying  
89 mechanisms behind these patterns.

90

91 The megabenthic communities of the offshore waters of the Gulf of Guinea region are  
92 poorly known (Le Loeuff, 1993; Le Loeuff and von Cosel, 1998; Lebrato and Jones,  
93 2009) compared to the Canary region to the north (Duineveld *et al.*, 1993a; Duineveld  
94 *et al.*, 1993b; Henriques *et al.*, 2002; Jones and Brewer, 2012; Keller and Pasternak,  
95 2002; Merrett and Domanski, 1985; Merrett and Marshall, 1981). The Benguela  
96 region to the south of the Gulf of Guinea has also received some attention,  
97 particularly on the shelf and slope (Roeleveld *et al.*, 1992; Roy *et al.*, 2007; Uriz,  
98 1988) as well as the abyss (Kroncke and Turkay, 2003; Levin and Gooday, 2001;  
99 Saiz-Salinas, 2007; Thandar, 1999; Vinogradova *et al.*, 1990; Zibrowius and Gili,  
100 1990). The Gulf of Guinea region is heavily exploited for natural resources, primarily  
101 hydrocarbon resources (Zabanbark, 2002) and fish (FAO Fishery Committee for the  
102 Eastern Central Atlantic, 1991) and is subject to high levels of anthropogenic impact

103 from pollution, mostly of terrestrial origin (Scheren *et al.*, 2002). The limited  
104 environmental information is mostly collected by oil and gas companies and not  
105 available in the scientific literature. However, it is crucial that baseline quantitative  
106 environmental information is available for successful management of this increasingly  
107 exploited ecosystem.

108

109 This paper provides the first description of deep-water megabenthic assemblages at a  
110 deep-water Nigerian site. Quantitative remotely operated vehicle (ROV) imaging  
111 allowed the effect of various seabed slopes on assemblage density, composition and  
112 diversity to be assessed. Specifically, the following hypotheses were tested: 1)  
113 increases in environmental heterogeneity associated with slope will increase  
114 megafaunal species richness, 2) increased slope will favour suspension feeding  
115 lifestyles at the expense of deposit feeding and hence change the relative abundances  
116 of these functional groups and 3) the combination of these effects will lead to  
117 differences in megafaunal assemblage structure between habitats with biologically  
118 significant variation in environmental conditions resulting from changes in slope.

119

## 120 2. Methods

121

### 122 2.1. Study Site

123

124 This study focuses on a knoll at the west of the Usan field (within Nigerian offshore  
125 oil prospecting license block 222), an area that will be developed for hydrocarbon  
126 production, located on the Nigerian continental margin in the Gulf of Guinea.

127 Environmental baseline surveys (Total E. & P. Nigeria Ltd., 2007) in the main Usan  
128 field (centred 03° 31.800' N 007° 26.400' E; slope < 1°) collected boxcore samples of  
129 seabed sediments. The silty clay sediment was comprised of silt ( $50.1 \pm 1.1$  %; mean  
130  $\pm$  standard deviation), clay ( $34.9 \pm 2.0$ %) and sand ( $15.1 \pm 1.0$  %), with an organic  
131 content of  $5.8 \pm 1.3$ % and a total organic carbon content of  $3.3 \pm 0.7$  %. Sediments  
132 contained abundant material of terrigenous origin (e.g. seeds, pollen, plant material).  
133 Sediments supported a macrofaunal (>0.5 mm) assemblage with low density ( $69 \pm 53$   
134 individuals m<sup>-2</sup>) and diversity (57 species). The macrofauna was dominated by  
135 molluscs (38.6%), arthropods (22.0%), protozoans (17.6%) and annelids (16.3%),

136 with the remainder comprised of echinoderms, cnidarians, poriferans and  
137 hemichordates (Total E. & P. Nigeria Ltd., 2007).

138

139 Shipboard measurements of seawater collected near the seabed at Usan had dissolved  
140 oxygen levels (mean = 5.84 mg L<sup>-1</sup> [54.7 % saturation], range = 4.41 [40.8 %] to 9.54  
141 [88.4 %] mg L<sup>-1</sup>) that were not hypoxic (dissolved oxygen is < 0.7 mg L<sup>-1</sup> (Helly and  
142 Levin, 2004)). *In situ* physical measurements of the near-bottom seawater (at 750 ±  
143 10 m water depth) made during this study showed low temperatures (5.32 ± 0.07 °C;  
144 mean ± standard deviation) and consistent salinities (34.76 ± 0.01).

145

## 146 2.2. Survey Design

147

148 Four habitats, each with different slope conditions (1°, 3°, 11° and 29°), were  
149 assessed at Usan (Figure 1) through the SERPENT project (Jones, 2009). The slope  
150 conditions were labelled 1°, 3°, 11° and 29°. For each slope condition an area was  
151 chosen within the Usan field using detailed bathymetric charts (Figure 1) that fulfilled  
152 the following criteria: constant slope, a depth between 740 and 760 m and a distance  
153 of at least 1 km from any drilling activity to ensure no effect of disturbance (Jones *et*  
154 *al.*, 2006). Three replicate remotely operated vehicle (ROV) video transects (200 m  
155 length) were performed at random locations within each slope condition (S1). Survey  
156 start points and survey direction were identified using a random number generator in  
157 Microsoft Excel. Transects were examined by plotting them onto the chart. Any  
158 transect that extended beyond the boundaries of identified areas was discarded and  
159 another generated using the same method. In the area of highest slope headings were  
160 constrained between 350 to 360°, 0 to 10° and 170 to 190° to maintain the depth  
161 range of transects but otherwise were random. Each transect was regarded as a  
162 sampling unit (i.e. all organism densities were totalled for each 200 m transect) and  
163 used in all subsequent analysis. Three replicate transects at four slope levels resulted  
164 in a total of 12 sampling stations. All positional information was recorded in  
165 Universal Transverse Mercator (UTM) zone 32 N based on the World Geodetic  
166 Society 1984 datum.

167

## 168 2.3. Data collection

169

170 Data were collected using an Oceaneering Millennium ROV equipped with a colour  
171 video camera (Insite Pacific Pegasus), sonar and ultra-short baseline navigation  
172 transponder. Cameras were mounted on a pan and tilt unit at the front of the ROV,  
173 which enabled oblique video to be taken. Before each transect the video was zoomed  
174 out to maximum extent and the camera was set to its most vertical angle (30° below  
175 the horizontal).

176

177 In every transect the ROV was run in a straight line, on a set bearing and at a constant  
178 speed ( $\sim 0.3 \text{ m s}^{-1}$ ). Vehicle altitude (distance from seabed to the base of the ROV)  
179 was kept constant at 1 m, which equated to a 143 cm camera altitude (from the centre  
180 of the camera). Transect width (mean of 1.72 m; max variation  $\pm 0.2 \text{ m}$ ) was  
181 calculated from the camera acceptance angles (Jones *et al.*, 2006). The camera  
182 horizontal acceptance angle (at full wide angle) was 55° and the vertical acceptance  
183 angle 43°. Transect width was also verified by passing over objects of known size on  
184 the seafloor. The optical resolution of the cameras permitted all organisms larger than  
185 50 mm to be reliably distinguished. In addition to the transects, previous ROV suction  
186 sampling at the nearby Akpo site (03°06.950' N 006°49.120' E) and a separate survey  
187 to carry out detailed video inspection of selected individual organisms aided species  
188 identifications (Jones *et al.*, 2006).

189

#### 190 2.4. Data Analysis

191

192 Video transects were replayed at half speed and all visible organisms were counted  
193 along the entire transect. Fauna were identified to the highest taxonomic resolution  
194 possible, in some cases to species. Megafauna that could not be identified to species  
195 were grouped into morphologically distinguishable entities (referred to as taxa). It  
196 should be emphasised that this approach may underestimate the number of species  
197 present. Colonial organisms were counted as single individuals. Infaunal species were  
198 counted if enough of their body was visible for identification. Benthic fish were  
199 recorded but not included in subsequent quantitative analysis. Megafauna were  
200 classified into deposit and suspension feeders based on the literature descriptions.

201

202 Four indices of diversity were calculated in order to assess both the dominance and  
203 species richness aspects of diversity (Magurran 2003, Gotelli & Colwell 2001). These  
204 were the number of taxa in a transect or group of transects (a simple measure of  
205 species richness, S), rarefied species richness (estimated species in 60 individuals:  
206  $ES_{(60)}$ ), evenness (as measured by Pielou's evenness,  $J'$ ) and Shannon-Wiener species  
207 diversity ( $H'$  base  $\log e$ ). Numbers of organisms were expressed as abundances  
208 (numbers in each sampling unit) or as densities ( $\text{no. m}^{-2}$ ). Diversity indices were  
209 calculated using PRIMER v6 (Clarke and Warwick, 2001).

210

211 The structure of the megabenthic assemblage was visualised using multidimensional  
212 scaling plots and sites compared using multivariate community analysis, specifically  
213 PERMANOVA (Anderson, 2001) and Multivariate dispersion analysis (Anderson,  
214 2006). Multivariate community analysis was based on abundances of all taxa, a fourth  
215 root transformation being applied to buffer the influence of dominant taxa (Field *et*  
216 *al.*, 1982). Similarities were calculated using Bray-Curtis coefficients (Bray and  
217 Curtis, 1957). The similarity values were subjected to both classification (hierarchical  
218 group-average clustering) and ordination (non-metric multi-dimensional scaling)  
219 using the software PRIMER v6 (Clarke and Warwick, 2001). PERMANOVA and  
220 Multivariate dispersion analysis were carried out using the 'adonis' and 'betadisper'  
221 functions respectively using the R package Vegan (Oksanen *et al.*, 2011) in the R  
222 programming environment (R Development Core Team, 2010).

223

224 Data were analysed following one-way analysis of variance (ANOVA) design with  
225 slope as a fixed factor. This was implemented in the univariate case by generalised  
226 linear models and in the multivariate case by one-way PERMANOVA (Anderson,  
227 2001). Independent generalised linear models were developed (Dobson and Barnett,  
228 2008) to examine whether the taxon richness (number of species in a transect) and  
229 density (as numbers of epibenthic invertebrates in a transect) of both suspension and  
230 deposit feeding taxa could be explained by the seabed slope (treated as categorical  
231 data). The residual deviance for the count data (48.44 for suspension feeders; 97.26  
232 for deposit feeders) was greater than the residual degrees of freedom (8 for both),

233 indicating overdispersion. The models were, therefore, fitted with quasi-Poisson  
234 errors. The models for species richness, evenness and species diversity were fitted  
235 with Gaussian errors. Models were fitted using the R function glm and the ANOVA  
236 function of the R package CAR (companion to applied regression) (Fox and  
237 Weisberg, 2011).

238

### 239 3. Results

240

241 The seabed was almost entirely composed of fine grain-sized sediment, no individual  
242 grains were visible in video (Figure 2), even when fully zoomed in. This suggested  
243 that the largest possible grain size is fine sand (< 0.5 mm) but observations of  
244 resuspension indicate that it was finer and classified as mud (< 125 µm). Hard  
245 substrata, composed of igneous rock (identified from samples), were visible within  
246 the areas of highest slope. These hard surfaces provided habitat for numerous  
247 specialist taxa (Table 1).

248

#### 249 3.1. Nature of the benthic community

250

251 A total of 24 invertebrate megafaunal taxa representing six phyla were observed in the  
252 video transects at Usan (Table 1, Figure 3). In terms of species richness and numerical  
253 abundance, echinoderms were most abundant: 64% of the fauna were accounted for  
254 by 10 echinoderm taxa. Although eight cnidarian taxa were identified, they only  
255 represented 4% of the total density. Crustaceans were numerically important (31%  
256 total fauna) but only represented by three taxa, one of which, a galatheid, accounted  
257 for the vast majority of individuals. Of lesser importance were the poriferans,  
258 molluscs and enteropneusts, all with only one observed taxon and together  
259 representing <1% of the total invertebrates.

260

261 The regular echinothurid echinoid *Phormosoma placenta* was overwhelmingly  
262 dominant, particularly in the flatter areas, accounting for 53% of the invertebrates  
263 observed. Two other taxa were numerically important; the galatheid *Munidopsis* sp.



264 represented 29% of megafauna and an unidentified large ophiuroid represented 8%.  
265 The other taxa observed were each of low abundance (<3% of megafauna).

266

267 Although not considered further in this analysis, fish were observed at all the sites  
268 (S2). A small, dark-coloured, midwater gonostomatid fish was most abundant  
269 representing over 47 % of the fish fauna. The true benthic lophiiform *Dibranchus* sp.  
270 was common and represented 27% of the fish. The other major taxon was the  
271 nettastomatid anguilliform *Nettastoma melanura* which accounted for 18% of the fish.  
272 The demersal grenadier *Corphaenoides* sp. and the morid gadiform *Laenomena*  
273 *laureysi?* each represented around 2% of the fish seen in the video records.

274

## 275 3.2. Variation between habitats

276

### 277 3.2.1. Faunal density

278

279 Faunal density varied between habitats of different slope, with lower total densities in  
280 areas of higher slope. When total density is split into more ecologically meaningful  
281 units, based on feeding mode, the trends were even clearer (Figure 4). Deposit feeders  
282 made up the majority of the megafauna observed; however, when analysed alone,  
283 densities of deposit feeders decreased significantly with greater slopes (L-ratio =  
284 16.09, d.f. = 3,  $p < 0.01$ ). Densities of suspension feeders were very low except at the  
285 habitat with the highest slope; even here the density was less than half ( $0.17 \text{ m}^{-2}$ ) that  
286 of deposit feeders ( $0.40 \text{ m}^{-2}$ ). The increase in deposit feeder densities with slope was  
287 significant (L-ratio = 35.41, d.f. = 3,  $p < 0.001$ ).

288

289 Of the major taxa, *Phormosoma placenta* had higher densities at low slope sites (L-  
290 ratio = 16.11, d.f. = 3,  $p < 0.01$ ) as did the galatheid *Munidopsis* sp. (L-ratio = 88.37,  
291 d.f. = 3,  $p < 0.001$ ). Ophiuroid densities were significantly higher in areas of higher  
292 slope (L-ratio = 24.88, d.f. = 3,  $p < 0.001$ ).

293

### 294 3.2.2. Megafaunal diversity and assemblage structure

295

296 The slope-related differences in the habitat had a significant effect on the number of  
297 taxa found (Figure 4; L-ratio = 9.33, d.f. = 3,  $p < 0.05$ ). Pairwise tests, however, only  
298 revealed significant differences between the habitat with the lowest slope ( $1^\circ$ ) and the  
299 highest slope ( $29^\circ$ ). The principal difference in the diversity of sites was caused by the  
300 presence of obligate epilithic species at the sites where hard substratum was exposed  
301 (see Table 1). In soft sediment areas there was some variation in species complement  
302 resulting from the apparently random presence or absence of rare species.

303

304 Species diversity indices (Figure 4) revealed that the species richness element of  
305 diversity ( $ES_{(60)}$ : L-ratio = 35.42, d.f. = 3,  $p < 0.001$ ) and the evenness component ( $J'$   
306 L-ratio = 66.14, d.f. = 3,  $p < 0.001$ ) showed a highly significant positive linear  
307 relationship with increasing slope of the habitat. As would be expected, a combined  
308 index showed similar patterns with slope ( $H'$ ; Figure 4). There were significant  
309 pairwise differences between all the habitats ( $p < 0.05$ ) in  $ES_{(60)}$ ,  $J'$  and  $H'$  except  
310 between 1 and 3 degrees in the combined Shannon-Wiener Index ( $p = ns$ ).

311

312 Overall, multivariate community similarity was significantly different between  
313 habitats of different slope (PERMANOVA:  $F = 9.55$ , d.f. = 1, 11,  $p < 0.001$ ; Figure  
314 5). Multivariate community similarity was high ( $> 60\%$ ) and between-site dispersion  
315 low between the habitats with lower slope ( $1$ ,  $3$  and  $11^\circ$ ), whereas the habitat with  
316 highest slope ( $29^\circ$ ) was more heterogeneous (Multivariate dispersion analysis:  
317 average distance to centroid 0.08 for  $1^\circ$ ; 0.14 for  $3^\circ$ ; 0.16 for  $11^\circ$  and 0.30 for  $29^\circ$ ;  
318 differences not significant in permutation test  $F = 2.57$ , d.f. = 3,  $p = 0.13$ ). Two sites  
319 (29B and 29C) formed a distinct group (with 77.5 % similarity) and one site (29A)  
320 was intermediate between the highest and lower slope sites, having slightly higher  
321 affinity with the lower slope sites (similarity 58.8%) than with the higher slope sites  
322 (similarity 35.9%).

323

## 324 4. Discussion

325

326 4.1. General characteristics of the megafaunal assemblages at Usan

327

328 Knowledge of West African megafauna is limited, making it difficult to compare the  
329 assemblage of invertebrates found at Usan to those at other locations. However, the  
330 common species are known and the limited evidence suggests they are abundant off  
331 West Africa. *Phormosoma placenta* is a common, often dominant, species on both  
332 sides of the Atlantic (Jones and Brewer, 2012; Laguarda-Figueras *et al.*, 2005;  
333 Sanchez *et al.*, 2008). The large ophiroid observed at Usan is very similar to a  
334 species found off Mauritania (Jones and Brewer, 2012), Ivory Coast and Angola  
335 (author's observation; <http://archive.serpentproject.com/151/>), while a galatheid  
336 resembling the species observed in the present study has been seen in images obtained  
337 off Ivory Coast (Lebrato and Jones, 2009). It should be noted that even generic  
338 differences are not always evident in photographs. The rarer species quantified in our  
339 survey, and those seen outside the transect areas, likely include new species.  
340 However, standard-resolution video and image data in general is not usually sufficient  
341 to resolve the details necessary for species-level taxonomy.

342

343 The density of the megafaunal assemblages at Usan seems to be low, but in the range  
344 of those found elsewhere (Figure 6). The nearest comparative area of an equivalent  
345 depth is located off Ivory Coast where megafaunal densities were over three times  
346 greater than at our study site. However, the Ivory Coast site experienced significantly  
347 enhanced nutrient inputs from pyrosome carcasses (Lebrato and Jones, 2009). Few  
348 other data are available for the East Atlantic at equivalent depths. Studies conducted  
349 in deeper areas reported a range of megafaunal densities (Figure 6) that are usually  
350 lower than at the Usan site. Of the deeper studies, only those areas that underlie  
351 highly productive surface waters, for example the eutrophic EUMELI site off  
352 Mauritania (Galeron *et al.*, 2000), have yielded comparable values.

353

354 4.2. Environmental consequences of differences in slope

355

356 Although four species were present at habitats with all the levels of slope investigated,  
357 ten of the taxa found at the habitat with the highest slope (29) were confined to this  
358 habitat. This habitat had exposed hard substrata and hence a unique community of  
359 epilithic megafauna. Most of the epilithic organisms were not found on soft sediments  
360 and many, for example gorgonians, had obvious morphological adaptations for  
361 attachment to rocky surfaces. Hard substratum communities are probably rare on the  
362 West African margin, having only been described off Mauritania where they are  
363 associated with corals (Colman *et al.*, 2005). Other studies of hard substrata near west  
364 Africa are on the mid-Atlantic ridge at non-vent (Gebruk *et al.*, 2010) and vent sites  
365 (Van Dover *et al.*, 2002), volcanic island groups, for example the Azores, or  
366 seamounts (Hall-Spencer *et al.*, 2007). The megafaunal assemblage found on hard  
367 substrata at Usan superficially resembles that found at non-vent hard substrata in the  
368 northern tropical Atlantic (in terms of faunal groups present) and from hard substrata  
369 in the deep sea in general (e.g. Lundsten *et al.*, 2009). However, without accurate  
370 species-level identifications either here or in the megafaunal literature generally,  
371 further patterns are difficult to assess.

372

373 The large reductions in density of deposit-feeding species at Usan with increases in  
374 habitat slope likely reflect reductions in food availability for deposit feeders. These  
375 patterns are unlikely to be related to the presence of hard substratum at the steepest  
376 slope site. Slope is expected to affect food availability in two ways. Firstly, increased  
377 slope will probably increase the lateral advection of food particles, reducing their  
378 residence times and hence availability for deposit feeders. Decreases in food  
379 availability have been repeatedly shown to be responsible for reductions in benthic  
380 megafaunal density in the deep sea (Galeron *et al.*, 2000; Thurston *et al.*, 1994).  
381 Secondly, increases in slope are likely to enhance local current speeds and hence lead  
382 to reductions in the deposition and increases in the winnowing of fine, nutritious  
383 particles (Levin *et al.*, 2001). Increased flow favours suspension feeding organisms  
384 over deposit feeders (Jumars and Nowell, 1984) and actively enhances recruitment,  
385 driving increased species density and elevated species richness (Palardy and Witman,  
386 2011).

387

388 Increases in slope were associated with increased overall megafaunal diversity at  
389 Usan despite a decrease in the number of deposit-feeding species in the habitat with  
390 the steepest slopes. There was slightly (although not significantly) higher diversity,  
391 and consistent changes in multivariate community composition, in areas of steep slope  
392 without hard substrata. In the absence of other factors, reduced food availability tends  
393 to lead to reductions in diversity (Levin *et al.*, 2001; Waide *et al.*, 1999), as  
394 demonstrated in the tropical Atlantic deep sea (Cosson *et al.*, 1997). Organic particles  
395 are more likely to settle and become available for deposit feeders at low slopes  
396 (Fontanier *et al.*, 2008). At high slopes resuspension and current-mediated lateral  
397 transport of organic material is likely (Schlacher *et al.*, 2007; Van Gaever *et al.*,  
398 2009), which may favour a suspension-feeding lifestyle. The trends in diversity  
399 observed at Usan are consistent with predictions based on food availability. Higher  
400 levels of organic matter may result in reduced diversity in areas, such as oxygen  
401 minimum zones, where the organic inputs are already high and associated with  
402 oxygen depletion (Levin *et al.*, 2001), which was not observed at Usan. In addition to  
403 influencing the organic content of the sediment, increases in slope are also likely to  
404 affect the substratum heterogeneity. Sediment grain size will likely become coarser  
405 and potentially more heterogeneous, increasing niche availability and hence deposit  
406 feeder diversity (Etter and Grassle, 1992; Wheatcroft, 1992), although this was not  
407 clear in the present study. In the Usan area the sites with steep slope have exposed  
408 hard substrata, presumably reflecting limited deposition. This increase in habitat  
409 heterogeneity is responsible for the clear and significant increases in diversity and  
410 changes in multivariate community composition at the steepest slope sites. An entirely  
411 different range of animals is able to colonise hard substrata and hence, where this is  
412 present, diversity is likely to increase (Levin *et al.*, 2001).

413

414 Deep-sea biology requires more detailed local-scale studies of faunal distribution in  
415 relation to habitat features. Physical gradients in biological assemblages associated  
416 with slope occur in many ecosystems (de Castilho *et al.*, 2006); this study extends  
417 these findings to the African deep sea. Considerable areas of the ocean margins have  
418 features of high topography and sloping seabed, such as described here. This study  
419 has shown clear reductions in deposit-feeding megafaunal density with slope. If this  
420 trend is typical for deep-water habitats, it should be incorporated into model estimates

421 of megafaunal densities, particularly on areas of elevated topography. Diversity of  
422 benthic megafauna does not display such a clear relationship with slope and is likely  
423 to be controlled by site-specific responses to changes in habitat heterogeneity and  
424 food availability.

425

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427

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441 6. References

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