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

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Abstract

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

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

1. Introduction

Habitat heterogeneity at local scales is a ubiquitous feature of bathyal continental margins and exerts a fundamental influence on the diversity and structure of benthic communities (Levin and Dayton, 2009). The ‘habitat heterogeneity hypothesis’ is one of the cornerstones of ecology (e.g. MacArthur and Wilson, 1967; Simpson, 1949). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Tews et al., 2004). Characterisation of the seabed in terms of terrain parameters, such as slope and aspect, is a potentially valuable tool for classifying the structural complexity of the seabed and delineating regions of seabed that may support particular fauna and therefore provide a distinct habitat (Wilson et al., 2007). These techniques, broadly classified as habitat mapping, have been successful in shallow waters (Lundblad et al., 2006) and are receiving increased attention in deep water (Jones and Brewer, 2012; Wilson et al., 2007). Slope is a commonly used and important parameter in these analyses, but direct assessment of changes in deep-water assemblages in relation to seabed slope have not (to the author’s knowledge) been assessed quantitatively. Flat areas tend to exhibit different seabed facies and support communities that are different to those inhabiting steeply sloping areas (Lundblad et al., 2006; Schlacher et al., 2007). Slope, as with depth, is not a direct environmental factor that controls biological communities; rather it is a useful proxy for correlated but unmeasured factors. In the case of slope, these environmental factors range across the scale of investigation but include a complex of environmental variables, primarily habitat heterogeneity (Schaff et al., 1992), local current flow (Noble and Mullineaux, 1989; Palardy and Witman, 2011), sedimentation, substratum type, food availability and colonisation (Butman, 1990; Butman et al., 1994; Gage, 1997). Shallow water
research suggests that these factors may lead to increases in density (Sebens, 1985), higher diversity (Palardy and Witman, 2011), elevated growth rates and changes in species distribution (Leichter and Witman, 1997) as well as functional changes in benthic communities, for example favouring suspension feeding over deposit feeding organisms (Jumars and Nowell, 1984). It is important to assess the role of slope-related factors in driving the structure of deep-water benthic faunal assemblages (Levin et al., 2001; Tyler, 1995), particularly in areas of high habitat complexity such as canyons (De Leo et al., 2010; Rowe et al., 1982) and seamounts (Clark et al., 2010; Genin et al., 1986).

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

The megabenthic communities of the offshore waters of the Gulf of Guinea region are poorly known (Le Loeuff, 1993; Le Loeuff and von Cosel, 1998; Lebrato and Jones, 2009) compared to the Canary region to the north (Duineveld et al., 1993a; Duineveld et al., 1993b; Henriques et al., 2002; Jones and Brewer, 2012; Keller and Pasternak, 2002; Merrett and Domanski, 1985; Merrett and Marshall, 1981). The Benguela region to the south of the Gulf of Guinea has also received some attention, particularly on the shelf and slope (Roeleveld et al., 1992; Roy et al., 2007; Uriz, 1988) as well as the abyss (Kroncke and Turkay, 2003; Levin and Gooday, 2001; Saiz-Salinas, 2007; Thandar, 1999; Vinogradova et al., 1990; Zibrowius and Gili, 1990). The Gulf of Guinea region is heavily exploited for natural resources, primarily hydrocarbon resources (Zabanbark, 2002) and fish (FAO Fishery Committee for the Eastern Central Atlantic, 1991) and is subject to high levels of anthropogenic impact
from pollution, mostly of terrestrial origin (Scheren et al., 2002). The limited environmental information is mostly collected by oil and gas companies and not available in the scientific literature. However, it is crucial that baseline quantitative environmental information is available for successful management of this increasingly exploited ecosystem.

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

2. Methods

2.1. Study Site

This study focuses on a knoll at the west of the Usan field (within Nigerian offshore oil prospecting license block 222), an area that will be developed for hydrocarbon production, located on the Nigerian continental margin in the Gulf of Guinea. Environmental baseline surveys (Total E. & P. Nigeria Ltd., 2007) in the main Usan field (centred 03° 31.800’ N 007° 26.400’ E; slope < 1°) collected boxcore samples of seabed sediments. The silty clay sediment was comprised of silt (50.1 ± 1.1 %; mean ± standard deviation), clay (34.9 ± 2.0%) and sand (15.1 ± 1.0 %), with an organic content of 5.8 ± 1.3% and a total organic carbon content of 3.3± 0.7 %. Sediments contained abundant material or terrigenous origin (e.g. seeds, pollen, plant material). Sediments supported a macrofaunal (>0.5 mm) assemblage with low density (69 ± 53 individuals m⁻²) and diversity (57 species). The macrofauna was dominated by molluscs (38.6%), arthropods (22.0%), protozoans (17.6%) and annelids (16.3%),
with the remainder comprised of echinoderms, cnidarians, poriferans and
hemichordates (Total E. & P. Nigeria Ltd., 2007).

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

2.2. Survey Design

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

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

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

2.4. Data Analysis

Video transects were replayed at half speed and all visible organisms were counted along the entire transect. Fauna were identified to the highest taxonomic resolution possible, in some cases to species. Megafauna that could not be identified to species were grouped into morphologically distinguishable entities (referred to as taxa). It should be emphasised that this approach may underestimate the number of species present. Colonial organisms were counted as single individuals. Infaunal species were counted if enough of their body was visible for identification. Benthic fish were recorded but not included in subsequent quantitative analysis. Megafauna were classified into deposit and suspension feeders based on the literature descriptions.
Four indices of diversity were calculated in order to assess both the dominance and species richness aspects of diversity (Magurran 2003, Gotelli & Colwell 2001). These were the number of taxa in a transect or group of transects (a simple measure of species richness, $S$), rarefied species richness (estimated species in 60 individuals: $ES_{(60)}$), evenness (as measured by Pielou’s evenness, $J'$) and Shannon-Wiener species diversity ($H'$ base log e). Numbers of organisms were expressed as abundances (numbers in each sampling unit) or as densities (no. m$^{-2}$). Diversity indices were calculated using PRIMER v6 (Clarke and Warwick, 2001).

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

Data were analysed following one-way analysis of variance (ANOVA) design with slope as a fixed factor. This was implemented in the univariate case by generalised linear models and in the multivariate case by one-way PERMANOVA (Anderson, 2001). Independent generalised linear models were developed (Dobson and Barnett, 2008) to examine whether the taxon richness (number of species in a transect) and density (as numbers of epibenthic invertebrates in a transect) of both suspension and deposit feeding taxa could be explained by the seabed slope (treated as categorical data). The residual deviance for the count data (48.44 for suspension feeders; 97.26 for deposit feeders) was greater than the residual degrees of freedom (8 for both),
indicating overdispersion. The models were, therefore, fitted with quasi-Poisson errors. The models for species richness, evenness and species diversity were fitted with Gaussian errors. Models were fitted using the R function glm and the ANOVA function of the R package CAR (companion to applied regression) (Fox and Weisberg, 2011).

3. Results

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

3.1. Nature of the benthic community

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

The regular echinothurid echinoid *Phormosoma placenta* was overwhelmingly dominant, particularly in the flatter areas, accounting for 53% of the invertebrates observed. Two other taxa were numerically important; the galatheid *Munidopsis* sp.
represented 29% of megafauna and an unidentified large ophiuroid represented 8%. The other taxa observed were each of low abundance (<3% of megafauna).

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

3.2. Variation between habitats

3.2.1. Faunal density

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

Of the major taxa, *Phormosoma placenta* had higher densities at low slope sites (L-ratio = 16.11, d.f. = 3, p < 0.01) as did the galatheid *Munidopsis* sp. (L-ratio = 88.37, d.f. = 3, p < 0.001). Ophiuroid densities were significantly higher in areas of higher slope (L-ratio = 24.88, d.f. = 3, p < 0.001).
3.2.2. Megafaunal diversity and assemblage structure

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

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

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

4. Discussion
4.1. General characteristics of the megafaunal assemblages at Usan

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

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

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

The large reductions in density of deposit-feeding species at Usan with increases in habitat slope likely reflect reductions in food availability for deposit feeders. These patterns are unlikely to be related to the presence of hard substratum at the steepest slope site. Slope is expected to affect food availability in two ways. Firstly, increased slope will probably increase the lateral advection of food particles, reducing their residence times and hence availability for deposit feeders. Decreases in food availability have been repeatedly shown to be responsible for reductions in benthic megafaunal density in the deep sea (Galeron et al., 2000; Thurston et al., 1994). Secondly, increases in slope are likely to enhance local current speeds and hence lead to reductions in the deposition and increases in the winnowing of fine, nutritious particles (Levin et al., 2001). Increased flow favours suspension feeding organisms over deposit feeders (Jumars and Nowell, 1984) and actively enhances recruitment, driving increased species density and elevated species richness (Palardy and Witman, 2011).
Increases in slope were associated with increased overall megafaunal diversity at Usan despite a decrease in the number of deposit-feeding species in the habitat with the steepest slopes. There was slightly (although not significantly) higher diversity, and consistent changes in multivariate community composition, in areas of steep slope without hard substrata. In the absence of other factors, reduced food availability tends to lead to reductions in diversity (Levin et al., 2001; Waide et al., 1999), as demonstrated in the tropical Atlantic deep sea (Cosson et al., 1997). Organic particles are more likely to settle and become available for deposit feeders at low slopes (Fontanier et al., 2008). At high slopes resuspension and current-mediated lateral transport of organic material is likely (Schlacher et al., 2007; Van Gaever et al., 2009), which may favour a suspension-feeding lifestyle. The trends in diversity observed at Usan are consistent with predictions based on food availability. Higher levels of organic matter may result in reduced diversity in areas, such as oxygen minimum zones, where the organic inputs are already high and associated with oxygen depletion (Levin et al., 2001), which was not observed at Usan. In addition to influencing the organic content of the sediment, increases in slope are also likely to affect the substratum heterogeneity. Sediment grain size will likely become coarser and potentially more heterogeneous, increasing niche availability and hence deposit feeder diversity (Etter and Grassle, 1992; Wheatcroft, 1992), although this was not clear in the present study. In the Usan area the sites with steep slope have exposed hard substrata, presumably reflecting limited deposition. This increase in habitat heterogeneity is responsible for the clear and significant increases in diversity and changes in multivariate community composition at the steepest slope sites. An entirely different range of animals is able to colonise hard substrata and hence, where this is present, diversity is likely to increase (Levin et al., 2001).

Deep-sea biology requires more detailed local-scale studies of faunal distribution in relation to habitat features. Physical gradients in biological assemblages associated with slope occur in many ecosystems (de Castilho et al., 2006); this study extends these findings to the African deep sea. Considerable areas of the ocean margins have features of high topography and sloping seabed, such as described here. This study has shown clear reductions in deposit-feeding megafaunal density with slope. If this trend is typical for deep-water habitats, it should be incorporated into model estimates.
of megafaunal densities, particularly on areas of elevated topography. Diversity of benthic megafauna does not display such a clear relationship with slope and is likely to be controlled by site-specific responses to changes in habitat heterogeneity and food availability.

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6. References


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Table 1: Invertebrate megafauna densities (no m⁻²) at each transect at Usan. Slope is represented by numbers: 1 = 1°, 3 = 3°, 11 = 11°, 29 = 29°. Site letters represent replicates. Asterisked taxa (*) are known to prefer hard substrata and double asterisked (**) only live on hard substrata (obligately epilithic). Deposit feeders (D) and suspension feeders (S) are labelled. See figure 3 for images of the taxa.

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FIGURES

Figure 1: Bathymetry of Usan area showing the position of ROV seabed transects. The lower panel shows the higher slope transects in more detail. The inset on the upper panel shows the position of the study site in the Gulf of Guinea. The length of the 200 m long ROV transects is drawn to scale.

Figure 2: Example pictures of seabed habitats with different slope found at Usan: A) 1° slope, B) 3° slope, C) 11° slope, D) soft-substratum area with 29° slope and E) hard-substratum area with 29° slope. Images A to D are images from the video transects cropped to show an approximately 0.5 m wide section of seafloor at the base of the image. Image E is a more oblique image cropped to show an approximately 1 m wide section of seafloor at the base of the image.

Figure 3: Examples of megafauna found at Usan: A) Hexactinellid (~150 mm diameter), B) White antipatharian (~200 mm height), C) Whip-like cnidarian (found on rocks, ~ 400 mm height), D) Whip-like cnidarian (found on sand, ~ 300 mm height), E) Gorgonian fan (~ 1m height), F) *Pennatulea* sp. (~300 mm height), G) Brisingid (arm length ~ 250mm), H) *Phormosoma placenta* (50-120 mm diameter), I) Red echinoid (70 mm diameter), J) White *Diadema* sp. (~150 mm diameter including spines), K) Ophiuroid (~150 mm arm-tip to arm-tip), L) Galatheid (up to 100 mm length), M) *Prawn* (~100 mm total length), N) *Cerianthid?* (~ 100 mm total diameter), O & P) *Lithodid crab* (c.f. *Paralomis cristulata*, ~100 carapace width). * species observed but not seen in quantitative transects.

Figure 4: Response of megafaunal assemblage indices to slope at the Usan area, offshore Nigeria. A) Megafaunal invertebrate deposit (hollow circles) and suspension feeding (filled circles) assemblage total densities. B) Number of megafaunal invertebrate deposit (hollow circles) and suspension feeding (filled circles) taxa. C) Evenness of entire invertebrate megafaunal assemblage measured by Pielou’s evenness (J’). D) Shannon-Wiener (log base e) combined diversity index (H’) of entire invertebrate megafaunal assemblage. Errors bars on all graphs represent standard deviations and points represent the mean density of 3 replicates. For A) and B) the megafauna was separated into deposit (hollow circles) and suspension (filled circles) feeders.

Figure 5: Multidimensional Scaling Ordination of Bray-Curtis similarities (4th root transformed) of Usan Invertebrate megafaunal assemblage. Overlaid are similarity levels from hierarchical cluster analysis (as percentages). Slope is represented by numbers equating to the slope in degrees. Letters represent replicates.

Figure 6: Megafaunal density (no hectare⁻¹) compared with depth for the Eastern Atlantic. East Atlantic literature data from Bay of Biscay south to Angola (Feldt *et al.*, 1989; Galeron *et al.*, 2000; Kroncke and Turkay, 2003; Lebrato and Jones, 2009; Sibuet *et al.*, 1989; Sibuet *et al.*, 1984; Sibuet and Segonzac, 1985; Thurston *et al.*, 1994; Tietjen, 1992)