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First quantitative exploration of benthic megafaunal assemblages on the mid-oceanic ridge system of the Carlsberg Ridge, Indian Ocean

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There are few quantitative studies on deep-sea biodiversity from the Indian Ocean, particularly on the mid-ocean ridges (MOR). We investigated the benthic megafaunal community structure of the Indian Ocean MOR at the Carlsberg Ridge (CR) using underwater video observation by the Television Gripper (TVG) and Ocean Floor Observation System (OFOS) during a multidisciplinary scientific cruise in 2007. Our aim was to observe megafaunal assemblages and their variation with bottom substrate at different geological settings in the CR region. The fauna was identified at best possible taxonomic resolution from video images and data were quantified by photogrammetry. Variation of substratum type was greatest in the deeper areas of the CR region, with substrata varying from fine sediments to basalts. A total of eight substratum types and 90 megafaunal taxa, representing seven phyla, have been classified throughout the 10 transects. Faunal abundances ranged between 171.3 to 5.7 animals 1000 m^{-2}, with higher abundances at the shallower transects, in off-axial highs, and lower at deeper zones, on the rift valley wall and floor. Cnidarians were dominant at off-axial highs while echinoderms prevailed at rift valley floor transects. Other frequently encountered faunal components were poriferans and chordates, observed at shallower as well as deeper transects. This is the first detailed investigation of megafaunal assemblages from the Indian Ocean MOR.

Keywords: benthic megafauna, habitat heterogeneity, deep-sea, mid-oceanic ridges, Carlsberg Ridge, Indian Ocean

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INTRODUCTION

The deep sea is considered to be the largest biome on Earth and the benthic fauna represents the most abundant component of life in the deep sea (Priede *et al.*, 2013). Deep oceanic benthic species live mostly within soft sediments, although they include assemblages living on hard rocks of continental slopes, seamounts and mid-oceanic ridges. Mid-ocean ridges (MOR) are underwater chains of mountains that constitute the largest topographic feature on this planet, extending to 75,000 km in length (Garrison, 1993), and have attracted considerable attention for their enhanced biodiversity, fisheries and mineral resources (Fowler & Tunnicliffe, 1997; Clark *et al.*, 2010; Priede *et al.*, 2013). Earlier biological studies on MOR mostly focused on chemosynthetic environments (Van Dover, 2000), while comparatively few studies addressed heterotrophic fauna (Felley *et al.*, 2008; Molodtsova, 2013). However, the recent multinational project on 'Patterns and process of the Ecosystem of the Northern Mid-Atlantic' (MAR-ECO) (Bergstad & Godø, 2003; Bergstad *et al.*, 2008), part of the global Census of Marine Life (CoML) programme (McIntyre, 2010), has greatly increased knowledge of MOR environments.

The Carlsberg Ridge, the north-western limb of the Indian Ocean Ridge system, is one of the least studied oceanic ridge systems. Several geophysical and hydrographic surveys have been carried out (Laughton, 1967; Murton *et al.*, 2003; KameshRaju *et al.*, 2008; Ray *et al.*, 2008, 2012) in different segments of Carlsberg Ridge. However, there have been very few investigations of regional benthic fauna. Glasby (1971) explored the biological communities associated with the non-vent regions of the Carlsberg Ridge but no attempts have been made to quantify benthic faunal abundance or to link biological information with the environmental settings. Biological studies have mostly focused on the Kairei and Edmond fields near Rodriguez Triple Junction (Gamo *et al.*, 2001; Hashimoto *et al.*, 2001; Van Dover *et al.*, 2001).

The aim of this investigation was to quantify the megafaunal assemblages and to assess patterns in density between the depths and different seabed substrata in the CR region. In this article, we use broad-scale information on seafloor habitats and their associated megafaunal communities quantified from underwater video images collected in the CR region. This study was the first in the Carlsberg Ridge area to produce underwater images of benthic megafaunal communities in a quantitative manner.

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GEOLOGICAL SETTING OF THE STUDY AREA

The Carlsberg ridge, demarcating the north and north-western part of the Indian Ocean ridge system, is accreting at the divergent plate boundary between the Somalia–India and Arabian plates (McKenzie *et al.*, 1970). This is a typical slow spreading (half-spreading rate of 11 to 16 mm y^{-1}) ridge having a V-shaped well-defined deep (>4000 m) rift valley with a wide valley floor, steep sidewalls and several transform faults. Between 62°20′E and 66°20′E the Carlsberg Ridge has rugged topography with steep valley walls, ridge-parallel topographic fabric and axial volcanic ridges (KameshRaju *et al.*, 2008). Seabed depths along the CR range from 1600 m to more than 4000 m and likely represent a variety of ecological zones. The present investigation focuses on two ridge segments that include areas of an unusually large episodic event plume (CR-2003) between 5°10′ and 6°00′N (Murton *et al.*, 2003; Ray *et al.*, 2008) and potential hydrothermal activities between 3°30′ and 4°00′N (Ray *et al.*, 2012).

MATERIALS AND METHODS

In November 2007, the RV 'Sonne' (RVS-2) was used to survey two segments of the Carlsberg Ridge. As a part of this programme, we investigated benthic megafaunal communities and their distribution patterns among different geological settings (e.g. off-axial highs or mounds, valley wall and floor) of these two ridge segments (Figure 1). During the cruise, a TeleVision Gripper (TVG) and Ocean Floor Observation System (OFOS; Römer *et al.*, 2013) were operated over eight and three transects respectively (Table 1). EM120 multibeam bathymetry data were obtained on the same cruise and used to determine the survey locations. Three TVG transects (TVG 1, 2 and 3) were carried out to different parts of a large event plume area in the northern segment. The first survey (TVG 1) was along the deep valley floor while two others (TVG 2 and TVG 3) were on the corner highs near a transform fault. Another five surveys (TVG 4, 5, 6, 7 and 8) were in the southern segment, mostly over the deep valley floor (depth >3000 m). All three OFOS transects were located close to the rift valley wall near the valley floor. Owing to time limitations on the cruise video transect lengths were different (OFOS 1 and OFOS 3 were longer than OFOS 2 and TVG 3). All transects were included in quantitative analysis.

The benthic megafaunal communities were observed using video transects collected with TVG and OFOS. Both were operated from the starboard side of the ship. The OFOS seabed imaging platform was flown with a real-time video link to the surface (digital through a fibre optic lightweight launcher (LWL) cable). The position of OFOS was recorded continuously with reference to an Ultra-Short Baseline Navigation transponder. OFOS has three cameras: one PHOTOSEA 5000 stereo-camera (that obtains two simultaneous photographs), one colour video (DSPLMSC 2000 colours with parallel red lasers, mounted 100 mm apart, used for scaling) and one monochrome video camera (OSPREY 0111-6006 B/W) and lighting (4xROS QL 3000 and/or 2xDSPL Arc-light). The TVG system had a similar capacity to OFOS and had two video cameras (1xDSPLMSC 2000 colour, and 1xOSPREY OE 1390 monochrome digital

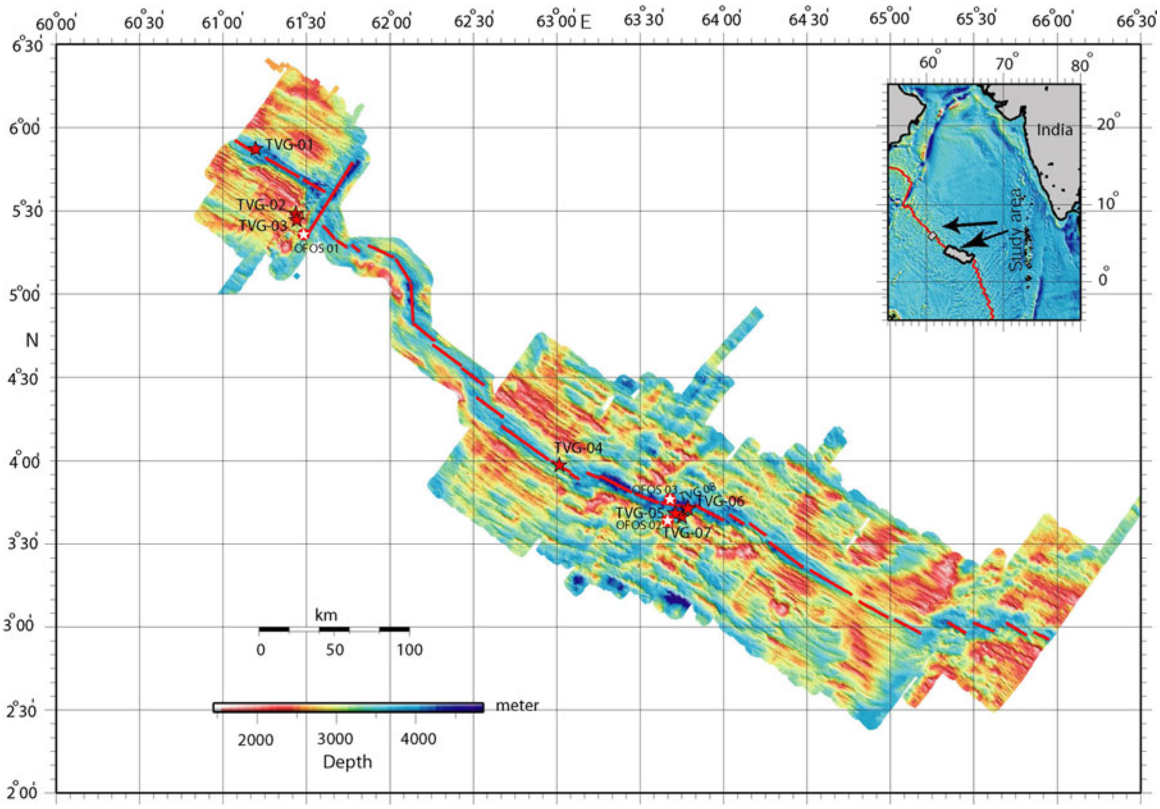

Fig. 1. Transect locations of the study area: Shallower transects TVG 2 and 3 and deeper transects TVG 1 and OFOS 1 located in the northern segments; other all deeper transects TVG 4, 5, 6, 7, 8 and OFOS 2 and 3 located in the southern segments in the Carlsberg Ridge.

Table 1. Details of underwater video observations and their geographic locations along with total number of fauna observed at each transect in Carlsberg Ridge, Indian Ocean.

Station ID	Date	Start location		End location		Depth range (m)	Bottom temperature (°C) (- CTD failed)	Transect length (km)	Area covered (km²)	Total number of individuals observed	Number of taxa
		Latitude (N)	Longitude (E)	Latitude (N)	Longitude (E)						
	Shallower										
	Off axial highs										
TVG2	25/10/2007	05°26.513′	61°26.524′	05°27.071′	61°26.193′	1643–1486	–	2.010	2.631	160	16
TVG3	25/10/2007	05°26.452′	61°26.578′	05°26.684′	61°26.459′	1834–1656	–	0.619	0.6537	114	14
	Deeper										
	Rift valley floor										
TVG1	24/10/2007	05°51.932′	61°11.203′	05°52.391′	61°11.695′	3676–3628	1.81	1.315	1.5096	44	4
TVG4*	03–04/11/2007	03°58.505′	63°01.000	03°58.556′	63°01.041′	3558–3365	1.90	0.201	0.2034	*	1
TVG5	11/11/2007	03°40.291′	63°44.794′	03°39.749′	63°45.032′	3413–3339	1.90	1.259	1.3245	21	9
TVG6	12/11/2007	03°40.325′	63°45.156′	03°39.821′	63°45.026′	3565–3436	1.90	2.038	2.2581	39	11
TVG7	13/11/2007	03°39.649′	63°44.474′	03°40.144′	63°44.907′	3669–3417	1.91	1.610	1.7581	61	16
TVG8	13/11/2007	03°40.356′	63°44.958′	03°40.009′	63°44.779′	3589–3529	1.91	2.077	2.4883	18	10
	Rift valley wall										
OFOS1	29–30/10/2007	05°13.647′	61°58.616′	05°14.304′	61°58.592′	3513–3548	1.82	10.6592	28.5985	1531	57
OFOS2	06/11/2007	03°47.932′	63°37.594′	03°47.758′	63°37.739′	3272–3291	1.95	0.3995	1.0805	12	8
OFOS3	06–07/11/2007	03°47.786′	63°37.736′	03°45.057′	63°37.265′	3288–4236	1.97	5.7405	15.4705	88	20

* Owing to technical problems the video was not clear for all of TVG 4. Two individuals were seen but we did not use the data for analysis of video transect TVG 4.

video), lighting (4xROS QL 3000) and telemetry. All the still photographs and video images were collected on digital versatile disc (DVD) at the surface. TVG was towed along the predefined track at a speed of ~0.5–0.7 knots while OFOS was operated at 0.2–0.5 knots. The cameras of both the systems obtained images at a height (altitude) of 1 to 5 m (depending on the seabed substratum) above the seabed. We have identified and quantified the faunal assemblages that are >1 cm in size and observed from an altitude less than 2.5 m from the seabed.

Image processing and data analysis

All megafauna were identified from images to a highest possible taxonomic resolution with additional help from experts (see acknowledgements). Owing to the nature of the image material, it was not possible to identify all animals to species level. Morphologically distinct organisms were identified and labelled with unique names referring to the taxon, such as Hexactinellida sp.1, Hexactinellida sp.2 or Holothuroidea sp.1 etc. Seabed substratum was classified into distinct 'substratum types', which may represent benthic habitats. Substratum types were identified based on seabed morphology and composition, such as rock type and sediment nature (Figure 2) and quantified by estimating the percentage of boulders, cobbles or fine sediment present, following the description of Hoff & Stevens (2005) (Table 2).

The substratum type, identity and number of all organisms were recorded along each transect. Positional information for each photograph was obtained from the navigation data. After analysing the navigational data, total transect length was measured manually in ArcGIS software. This measured length was used for subsequent area calculations. The width of the transect was ascertained from the laser scalers visible in each image (for OFOS) and from camera altitude (for TVG). For OFOS, the distance between laser scalers in 25–50 randomly selected frames was measured for each transect and the mean used to estimate the transect width. For TVG, transect width was calculated from mean camera altitude using the following equation:

$$\text{Width of transect, } W = 2 \times \tan\left(\frac{\alpha}{2}\right) \times \text{camera altitude}(H)$$

where, α is the angle of focal length (20°) of the camera.

The area coverage of each transect was estimated from the total length (L) and width (W) as follows:

$$\text{Area}(A) = L \times W$$

Based on the area calculated and after recording the individuals on the entire track, we estimated the faunal density at each transect.

Statistical analysis

Only those morphotypes that could be confidently identified were included in the analysis. To investigate how similarity between assemblages changes with the substratum type and bathymetric gradients in the Carlsberg Ridge, several multivariate analyses were conducted using PRIMER v6 (Clarke & Gorley, 2006). Following the general recommendations of Clarke & Gorley (2006), the Bray–Curtis similarity measure

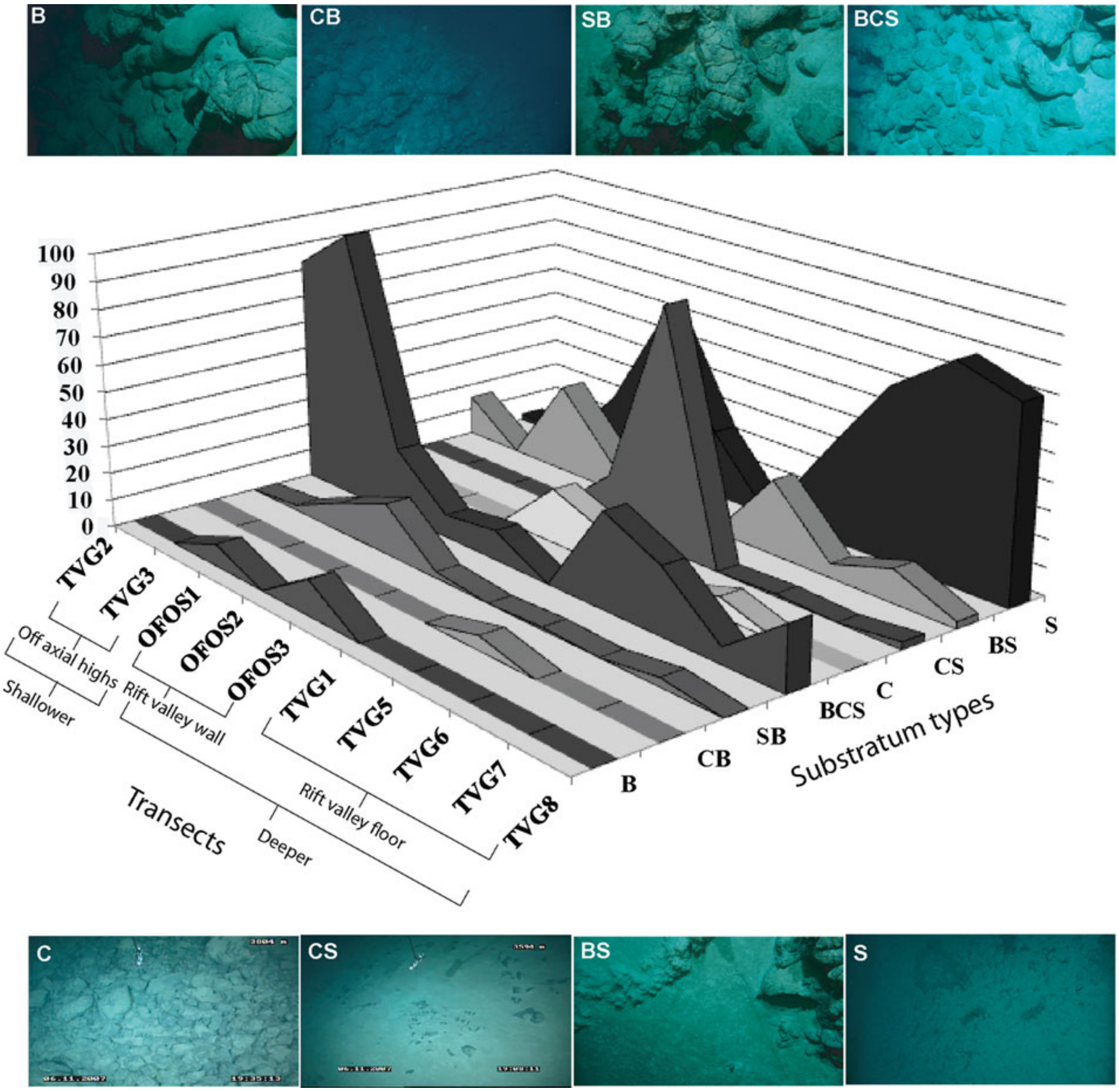

Fig. 2. Representative photographs of each substratum type and their distribution pattern along the transects in the study area. Y-axis represents percentage cover.

was employed to assess multivariate similarity and dissimilarity between transects based on log-transformed faunal abundance data. The differences between transect groups of substratum type were assessed with multivariate analysis and visualized using hierarchical clustering based on Bray–Curtis similarities of square root transformed data. The organisms that contributed most to the observed similarity within and dissimilarity among groups were assessed using SIMPER (similarity percentage).

Table 2. Composition of substratum types viewed from seafloor video images of the Carlsberg Ridge.

Substrate code	% of each substratum type			Substratum classification
	Boulder	Cobbles	Fine	
B	100	0	0	Boulder
CB	75	25	0	Cobble-Boulder
SB	75	0	25	Sediment-Boulder
BCS	25	25	50	Boulder-Cobble-Sediment (soft)
C	0	100	0	Cobble
CS	0	25	75	Cobble-Sediment (soft)
BS	25	0	75	Boulder-Sediment (soft)
S	0	0	100	Sediment (soft)

RESULTS

Distribution of substratum types

Substratum variability was greatest in the deeper areas of the rift valley, with substratum types varying from exposed pillow basalts to fine sedimentary cover on the rocky substratum. A total of eight different substratum types were classified over 10 TVG and OFOS transects located within our study area (Table 2). Substratum type distribution patterns and the percentage occurrence of substratum types for each transect (Figure 2) were variable.

Two shallower transects (TVG 2 and TVG 3), located on off-axial highs, have a seabed comprised of mostly basalts covered with sediments. The seafloor along the TVG 2 transect was predominantly the sedimented base of a basalt wall (BS), with some areas covered with sediment only. Transect of TVG 3 was mostly comprised of pillow/basalt blocks with sediments on a gradual slope (type BCS) with a small percentage of cracked pillow basalts with sediments (FB) observed.

All eight substratum types were found within the deeper areas. Most of the substrata in the region were sediment (S). Other seabed types were also fairly common, including gradually sloping sedimented seabed with basalt blocks (BCS), the sediment covered bases of basalt walls (BS), tallus on broken pillow fragments at the base of a scarp or small hillock (C) and basalt walls with sediment cover on ledges. Rarely there were thick mounds of pillow basalts with little sediments (SB). A maximum of seven substratum types were observed along the rift valley wall (at OFOS 3) while a minimum of two types were found at rift valley floor (at TVG 1).

Abundances and composition of megafaunal assemblage

A total of 2088 individuals from 90 taxa, representing seven phyla, were observed in the underwater video and still images in the two segments of the CR (Table 1; Supplementary Table 1). The population density varied between 5.7 and 171.3 animals $1000\ \mathrm{m}^{-2}$ with a mean of 38.0 ± 3.3 animals $1000\ \mathrm{m}^{-2}$ in the study area (Figure 3). A total of 272 individuals from 19 taxa were seen on an off-axial high observed in the shallower transects, and the remaining 1632 (69 taxa) and 186 (22 taxa) were observed on the rift valley wall and rift valley floor respectively. However, megafaunal densities were higher at shallower transects than deeper transects. Density varied from 60.8 to 171.3 animals $1000\ \mathrm{m}^{-2}$ (mean 116.1 ± 55.3) in the shallower transects on off-axial highs. In the deeper transects density varied from 5.7 to 53.5 animals $1000\ \mathrm{m}^{-2}$ (mean 23.8 ± 15.0) on the rift valley wall and 7.6 to 34.7 animals $1000\ \mathrm{m}^{-2}$ (mean 21.0 ± 4.9) on the valley floor. The highest density was observed along the off-axial highs transect of TVG 3, while the lowest was at the rift valley wall transect OFOS 3, which was the deepest transect of the study area (Figure 3). On average the megafaunal assemblage was dominated by cnidarians followed by poriferans and echinoderms. The cnidarians were mostly observed in shallower transects located in off-axial highs (Table 3). In both shallow transects the cnidarians were predominantly a black coral, *Stichopathes* sp., and the substratum type was mostly basalt blocks with cobbles and sediments (BCS). In contrast, the deeper transects contained a maximum of six megafaunal groups and were dominated by echinoderms followed by arthropods, poriferans, chordates, cnidarians and others (Table 3). Poriferans mostly appeared on pillow basalts on escarpments (B) and pillow basalts with sediments (BS), while cnidarians were found in higher densities on basalt blocks with sediments on a gradual slope (BSC). Echinoderms, arthropods and chordates were found in higher densities on the BCS substratum as well as sediment (S) rich areas. Other megafaunal groups, such as xenophyophores and annelids, were occasionally observed in both the segments.

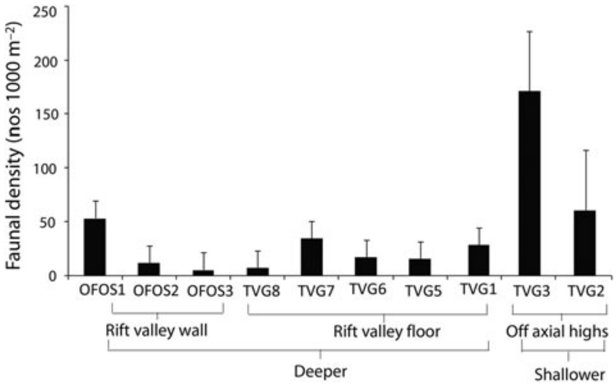

Fig. 3. Megafaunal density along the Carlsberg Ridge with different depths and geophysical settings.

Multivariate analysis: substratum types and faunal assemblages

The sites formed two distinct groups (Figure 4) when evaluated in terms of their substratum composition with 40% similarity from hierarchical clustering. Shallower transects (TVG 2 and TVG 3), located on the off-axial highs, formed Group A, where the boulder block with cobbles and fine sediments (BCS) substratum type contributed the highest similarity percentage (Supplementary Table 2) at this region. Substratum types that had mostly mixed sediments (e.g. BCS, BS, S) formed another cluster (Group B) with deeper transects on the rift valley wall and floor areas. The dissimilarity between the groups was observed principally because of differences in mixed substratum type BCS and S (sediments) substratum types, where BCS made the highest contribution at shallower depths and S highest contribution was at deeper depths (Figure 2).

The sites formed three distinct groups when analysed in terms of their megafaunal similarity (Figure 5). The multivariate analysis showed a clear distinction between the depths, geophysical settings, transects distances and substratum composition. One group (Group A) comprised the shallower transects (TVG 2 and TVG 3), the deeper transects on the rift valley floor (TVG 5, 6, 7 and 8) and on the rift valley wall (OFOS 2 and 3) made Group B and Group C respectively. Overall cnidarians *Stichopathes* sp. (Figure 6D), Brisingidae sp.2 (Figure 6C), Isididae sp.1 (Figure 6A), Actinaria sp.3 and poriferans Hexactinellida sp.9 were restricted to shallower transects in off-axial highs and responsible for >80% of the differences which separated Group A (Supplementary Table 3). The Arthropod *Cerataspis* sp. (Figure 6P) and holothurians *Peniagone* sp. (Figure 6L) and *Benthodytes* sp.2 were restricted to the rift valley floor transects (TVG 5, 6, 7 and 8) and were the major contributors (total 78%) to the similarity in Group B (Supplementary Table 3). The third group (Group C) was made by transects OFOS 2 and 3 owing to similarities in the density of *Ceratapsis* sp., Elpidiidae sp.1 and *Enypniastes exima* (contributed to 89% similarity). OFOS 1 and TVG 1 were the most remote deeper transects (a distance of OFOS 1 and TVG 1 from other deeper transects was over 50 km away from the southern segment).

Table 3. Abundance range (mean ± SD) of benthic megafaunal groups per 1000 m^2 area in the Carlsberg Ridge area.

Faunal groups	**Geophysical settings**		
	Off-axial highs (N = 2)	**Rift valley floor (N = 6)**	**Rift valley wall (N = 3)**
Porifera	8–23 (15.5 ± 10.6)	0–2 (0.6 ± 0.9)	1–44 (15.4 ± 24.3)
Cnidaria	37–125 (81 ± 62.2)	0–10 (2.1 ± 3.8)	0–7 (2.3 ± 3.9)
Echinodermata	11–18 (14.5 ± 4.9)	0–27 (8.8 ± 9.8)	1–3 (2 ± 0.7)
Arthropoda	0	0–12 (3.8 ± 4.4)	1–6 (2.8 ± 2.4)
Chordata	4–5 (4.5 ± 0.7)	0–10 (3.7 ± 3.8)	1–3 (1.2 ± 1.4)
Others (Annelidea and Xenophyophora)	0	0	0–0.1 (0.02)

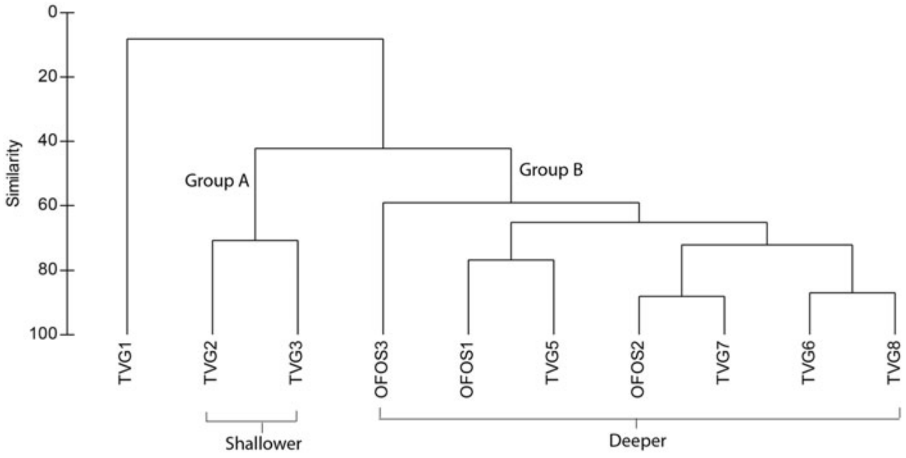

Fig. 4. Cluster analysis of substratum types at each transect along the CR.

DISCUSSION

All transects observed had basalts present. Some observations, for example, the C substratum types, included talus or broken pillow basal fragments at the base of small mounds, which may suggest tectonic activity in the area. Multibeam mapping of the Carlsberg Ridge between 62°20′E and 66°20′E (KameshRaju *et al.*, 2008) revealed rugged topography with steep valley walls, structures such as ridge-parallel topographic fabric and axial volcanic ridges, which correspond with features observed here. In this study, some substrata, such as sediments (S) and exposed basalts in thick sediment-covered plain (CS), were mostly covered with pelagic sediments, reworked by benthic fauna (such as observed at transect TVG 7). Similar types of substratum and suggested benthic activity have previously been observed in underwater photographs along the Carlsberg Ridge (Laughton, 1967) and along the Mid-Atlantic Ridge (Bell *et al.*, 2013, 2016). The general morphology of the Carlsberg Ridge sections used in the present study is similar to the Mid-Atlantic Ridge (MAR) between the Kane and Atlantis transform (KameshRaju *et al.*, 2008).

In the present study higher mean faunal density was observed in shallower transects located at off-axial highs,

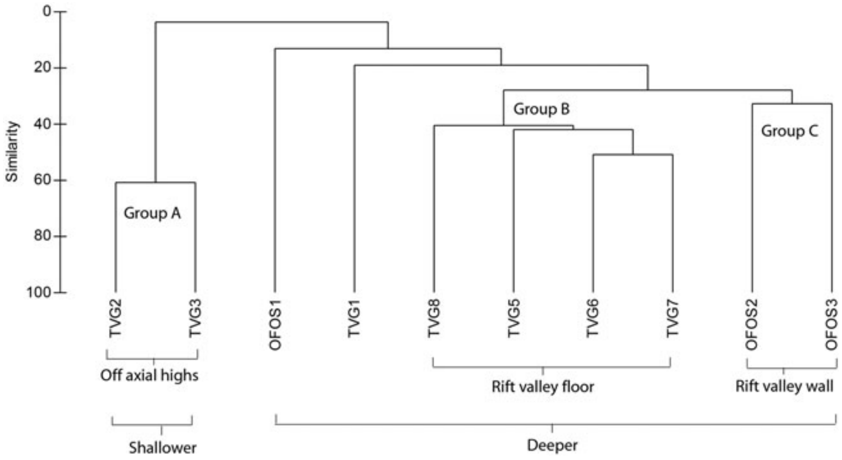

Fig. 5. Cluster analysis of megafaunal assemblages at each transect along the CR.

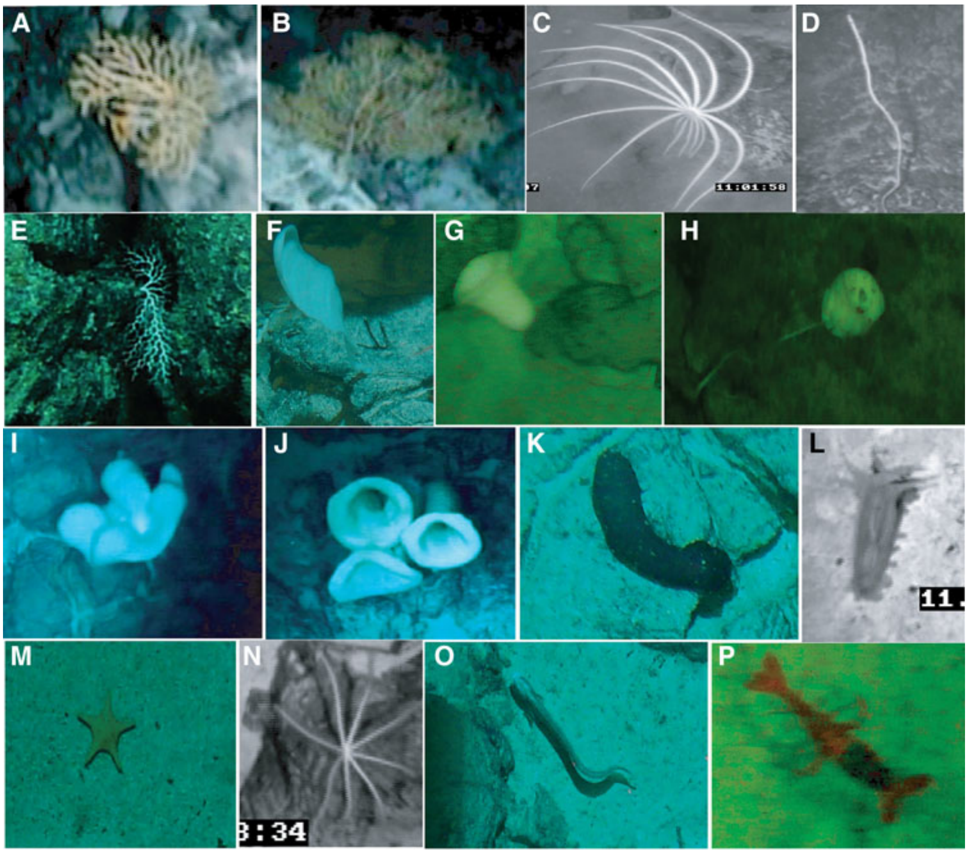

Fig. 6. Underwater images of benthic megafauna along the Carlsberg Ridge. *Shallower*: (A) Isididae sp.1; (B) Isididae sp.2; (C) Brisingidae sp.2; (D) *Stichopathes* sp.; *Deeper*: (E) *Stylasterine* sp.; (F) Aulocalycidae glass sponge; (G) *Hyalonema* sp.; (H) Bolosominae sponge; (I) *Crateromorpha* sp.; (J) Rossellidae glass sponge; (K) *Benthodytes* sp.; (L) *Peniagone* sp.; (M) Asteroid sp.1; (N) Brisingidae sp.1; (O) Anguilliformes sp.2; (P) *Cerataspis* sp.

while comparatively lower density and higher diversity were observed at the deeper transects. The western flanks of the Carlsberg Ridge around 300 km east of the study area and a little deeper (3472–3990 m) have extensive biological activity, characterized by large-scale burrowing of sediment and the appearance of worm casts, ophiuroids and holothurians (Glasby, 1971). However, no quantitative benthic megafaunal data are available to compare with the present study. Comparatively fewer species are recorded in the present study than on the MAR, probably owing to the relatively low sampling effort on the CR. More than 650 species of benthic invertebrate megafauna were recorded by physical sampling and underwater images on the MAR, of which 112 cnidarians and 35 poriferans were found specifically on hard substrata (Vecchione *et al.*, 2010). In the present study, density decreased with increasing depth. This is expected as decreases in faunal abundance with depth occur in most deep-sea communities investigated (e.g. Carney, 2005; O'Hara, 2008; Williams *et al.*, 2010), probably as a result of the exponential decline in food supply with depth (Lutz *et al.*, 2007).

In the present study Cnidarians, such as *Stichopathes* sp. (a sessile organism), were predominantly observed on rocks at shallower transects respectively, which mostly comprised basalt with cobble and sediments substratum BCS. Deep-sea poriferans and cnidarians are suspension feeding sessile fauna, often found on hard substrata, and typically live in areas with locally enhanced water currents to increase supply of food particles (Hogg *et al.*, 2010). These factors, with the availability of hard substratum habitat, determine their abundance and distribution (Rice *et al.*, 1990) here and on the MAR (Felley *et al.*, 2008).

At the deeper sites, where substrata were mostly sediments (particularly Sand CS substratum types at the deep valley floor), echinoderms and arthropods were common. Small-scale distribution patterns of deep-sea megafauna in the region of the Charlie-Gibbs fracture zone of the MAR showed holothurians mostly occurred on sediment-covered plains (Felley *et al.*, 2008; Alt *et al.*, 2013). Holothurians are deposit feeders reworking sedimentary particles (Gray, 1974; Rowe *et al.*, 1974), so this is not surprising.

The multivariate analysis revealed differences in megafaunal assemblages that appear to be associated with depth (or covariates such as food supply; Lutz *et al.*, 2007) and geophysical setting, as has been found on other topographic features in the deep sea (Jones & Brewer, 2012; Jones *et al.*, 2013; Priede *et al.*, 2013; Durden *et al.*, 2015; Bell *et al.*, 2016). There are also distinct differences in the megafaunal assemblages present on different substratum types. It is not possible to determine if the differences between the shallower and deeper areas are as a result of different substrata or other depth-related differences, such as differences in food supply (Lutz *et al.*, 2007).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at http://dx.doi.org/10.1017/S0025315416000515.

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