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

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Abstract
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 substrata at different geological settings in CR region. The fauna were 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 8 substratum types and 90 megafaunal taxa, representing 7 phyla, were identified have been classified throughout the eleven transects. Faunal abundances ranged between 171.3 to 5.7 animals Per 1000 m², with higher abundances at the shallower transect in off axial highs and lower at deeper zones in 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.
INTRODUCTION
The deep sea is considered as the largest biome on Earth and the benthic fauna represent the most abundant component of life in the deep sea. 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 attracted considerable attention for their fabulous 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 global Census of Marine Life (CoML) program (McIntyre, 2010), has greatly increased knowledge on 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; KameshRaju et al., 2008; Murton et al., 2003, 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 other ecological settings. Biological studies have mostly focused at the Kairei and Edmond fields near Rodriguez Triple Junction (Hashimoto et al., 2001; Gamo 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 bottom substrata in the CR region. In this paper 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.

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/yr) ridge having a V-shaped well-defined deep (> 4000 m) rift valley with a wide valley floor, steep side-walls 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 1600m to more than 4000m 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., 2012) and potential hydrothermal activities between 3°30’ and 4°00’N and (Ray et al., 2012).

**MATERIAL 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 program 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 Tele Vision Gripper (TVG) and Ocean Floor Observation System (OFOS) were operated over 8 and 3 transects respectively (Table 1). EM120 multi-beam 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 within different parts of large event plume area in the northern segment (Fig. 1). 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.

The benthic megafaunal communities were observed using video transects collected with the camera attached 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 fiber 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 similar capacity to OFOS and had two video cameras (1xDSPLMSC 2000 colour, and 1xOSPREY OE 1390 monochrome digital 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 the speed of about 0.5 to 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 at highest possible taxonomic resolution with additional help from experts (see acknowledgements). Owing to the nature of image material, it was not possible to identify all animals to species level. Morphologically distinct organisms were identified and labelled by unique names referring to the taxon, such as Hexactinellida sp1, Hexactinellida sp2 or Holothuroidea sp1 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; Table 2).

The substratum type, presence and identity of all organisms was 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 to 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:

\[ W = 2 \times \tan \left( \frac{\alpha}{2} \right) \times \text{camera altitude} \]

Where, \( \alpha \) is 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, 2006). Following the general recommendations of Clarke and Warwick (2001), the Bray-Curtis similarity measure was employed to assess multivariate similarity and dissimilarity between transects based on log-transformed faunal abundance data. The differences between transects groups of substratum type was assessed with multivariate analysis and visualized using non-metric Multi-Dimensional Scaling (nMDS). The organisms that contributed most to the observed similarity within and dissimilarity among groups were assessed using SIMPER (similarity percentage).

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 rocky substratum. A total of 8 different substratum types were classified over eleven 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 & 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 8 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 minimum of two types were found at rift valley floor (at TVG 1).
Abundances and composition of megafaunal assemblage

A total of 2090 individuals (13% at shallower and 87% at deeper areas) from 90 taxa, representing 7 phyla, were observed in the underwater video and still images in the two segments of the CR (Table 1; Suppl. Table 1). The population density varied between 5.68 and 171.34 animals 1000 m$^{-2}$ with a mean of $37.98 \pm 3.31$ animals 1000 m$^{-2}$ in the study area (Figure 3). 272 of individuals were seen on an off-axial high observed in the shallower transects, and the remaining 1632 and 186 were observed on rift valley wall and rift valley floor respectively. However, megafaunal densities were higher at shallower transects than deeper transects. Density varied from 60.81 to 171.34 animals 1000 m$^{-2}$ (mean $116.07 \pm 55.26$) in the shallower transects and from 53.53 to 5.68 animals 1000 m$^{-2}$ (mean $20.63 \pm 15.98$) in the deeper transects. The highest density was observed along off axial highs transect of TVG 3, while the lowest was at rift valley wall transect OFOS 3 which was the deepest transect of the study area. Number of taxon recorded from each transect shown in 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, Chordatas, 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 abundances on basalt blocks with sediments on a gradual slope (BSC). Echinoderms, arthropods and chordates were found higher on the BCS substratum as well as sediment (S) rich areas. Other megafaunal groups, such as xenophyophores and Annelida, were occasionally observed in both the segments.

Multivariate analysis: faunal assemblages in each substratum type

The sites formed two distinct groups, when evaluated in terms of their substratum composition (with 40% similarity from hierarchical clustering; Figure 4. Shallower transects (TVG2 and TVG3), located on the off-axial highs, formed Group 1, where the basalt blocks with sediments (BCS) substratum type contributed the highest similarity percentage (Suppl. Table 2) at this region. Substratum types that had mostly mixed sediments (e.g., BCS, SB, BS, S) formed another cluster (Group 2) with deeper transects on the rift valley wall and floor
areas. Dissimilarity between the groups was observed principally because of differences in mixed substratum type BCS and S (sediments) substratum types, where BCS made 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 made a clear distinction between the shallow and the deep areas (<5% similarity from cluster analysis). One group (Group A) comprised the shallower transects (TVG 2 & TVG 3) and the deeper transects OFOS 2 & 3 located in rift valley wall and TVG 5, 6, 7 & 8 in rift valley floor made Group B and Group C. Overall Stichopathes sp., Brisingidae sp2, Isididae sp1, Actinaria sp3 and Hexactinellida sp 9 (Figure 6) were restricted to shallower transects and responsible for >90% of the differences which separated Group A. Plesiopenaeus sp, fish Ophidiid sp1, Peniagone sp and Benthodytes sp2 were restricted to the rift valley floor transects TVG 5, 6, 7 & 8 and the major contributors (total 78%) to similarity in Group B (Suppl Table 3). The third Group C was made by transects OFOS 2 & 3 owing to similarities in density of Plesiopenaeus sp, Elpidiidae sp1 and Enypniastes exima (contributed to 89% similarity). OFOS 1, TVG 1 and TVG 4 were the most remote deeper transects (distance of OFOS 1 and TVG 1 from other deeper transects was over 50 km away from the southern segment) and TVG 4 only had a short observation period (35 minutes).

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 at the area. Multi-beam 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 TVG7). 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). 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, 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, brittle stars and holothurians (Glasby, 1971). However, no quantitative benthic megafaunal data are available to compare to 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 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 species), 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, mainly found to settle on hard substrata, and live in areas with local water currents to supply food particles from surface ocean (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 S and 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 megafaunal assemblages of our study area are distinct between the shallow and deeper water areas. 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).
In the present study 90 taxa were recorded, although most of them were not identified to species level, it would seem likely that some of these may be new to science. In dredge samples collected at the Carlsberg Ridge in 2009 a new genus and species of hexactinellid sponge was discovered (Sautya et al., 2011). In the southern South Atlantic MAR system (see Polar Biology, 2006: 29, special issue) benthic diversity was much higher than previously recorded for the area especially for echinoderms, molluscs, cheilostome bryozoans and amphipods and many of these records were new to the science. About 10% of species in MAR-ECO epibenthic invertebrate collections, made in the northern MAR, appeared to be new to the science (Vecchione et al., 2010). As the Carlsberg Ridge is one of the less studied areas of mid-ocean ridge in the world ocean, there is huge potential for new discovery.

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REFERENCES


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

<table>
<thead>
<tr>
<th>Station ID</th>
<th>Start Location</th>
<th>End Location</th>
<th>Depth range (m)</th>
<th>Bottom temperature (°C) (* CTD failed)</th>
<th>Transect length (km)</th>
<th>Area covered (km²)</th>
<th>Total number of individuals observed</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shallower</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Off axial highs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TVG3</td>
<td>25/10/2007</td>
<td>05° 26.452’</td>
<td>61° 26.578’</td>
<td>05° 26.684’</td>
<td>61° 26.459’</td>
<td>1834 - 1656</td>
<td>*</td>
</tr>
<tr>
<td><strong>Deeper</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rift valley floor</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TVG1</td>
<td>24/10/2007</td>
<td>05° 51.932’</td>
<td>61° 11.203’</td>
<td>05° 52.391’</td>
<td>61° 11.695’</td>
<td>3676 – 3628</td>
<td>1.81</td>
</tr>
<tr>
<td>TVG4*</td>
<td>03-04/11/2007</td>
<td>03° 58.505’</td>
<td>63° 01.000’</td>
<td>03° 58.556’</td>
<td>63° 01.041’</td>
<td>3558-3365</td>
<td>1.90</td>
</tr>
<tr>
<td>TVG5</td>
<td>11/11/2007</td>
<td>03° 40.291’</td>
<td>63° 44.794’</td>
<td>03° 39.749’</td>
<td>63° 45.032’</td>
<td>3413 - 3339</td>
<td>1.90</td>
</tr>
<tr>
<td>TVG6</td>
<td>12/11/2007</td>
<td>03° 40.325’</td>
<td>63° 45.156’</td>
<td>03° 39.821’</td>
<td>63° 45.026’</td>
<td>3565 - 3436</td>
<td>1.90</td>
</tr>
<tr>
<td>TVG7</td>
<td>13/11/2007</td>
<td>03° 39.649’</td>
<td>63° 44.474’</td>
<td>03° 40.144’</td>
<td>63° 44.907’</td>
<td>3669 - 3417</td>
<td>1.91</td>
</tr>
<tr>
<td>TVG8</td>
<td>13/11/2007</td>
<td>03° 40.356’</td>
<td>63° 44.958’</td>
<td>03° 40.009’</td>
<td>63° 44.779’</td>
<td>3589 - 3529</td>
<td>1.91</td>
</tr>
<tr>
<td><strong>Rift valley wall</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OFOS1</td>
<td>29-30/10/2007</td>
<td>05° 13.647’</td>
<td>63° 58.616’</td>
<td>05° 14.304’</td>
<td>63° 58.592’</td>
<td>3513 - 3548</td>
<td>1.82</td>
</tr>
<tr>
<td>OFOS2</td>
<td>06/11/2007</td>
<td>03° 47.932’</td>
<td>63° 37.594’</td>
<td>03° 47.758’</td>
<td>63° 37.739’</td>
<td>3272 - 3291</td>
<td>1.95</td>
</tr>
<tr>
<td>OFOS3</td>
<td>06-07/11/2007</td>
<td>03° 47.786’</td>
<td>63° 37.736’</td>
<td>03° 45.057’</td>
<td>63° 37.265’</td>
<td>3288 - 4236</td>
<td>1.97</td>
</tr>
</tbody>
</table>

* Owing to technical problems the video was not clear for all of TVG 4. We only used video collected between 23:58 to 00:33 for qualitative assessment of substratum and faunal assemblages.
Table 2. Composition of substratum types viewed from seafloor video images of the Carlsberg Ridge.

<table>
<thead>
<tr>
<th>Substrate code</th>
<th>Boulder</th>
<th>Cobbles</th>
<th>Fine</th>
<th>Substratum classification</th>
<th>Substratum description</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>Boulder</td>
<td>Pillow basalt with tubular shape associated with escarpment</td>
</tr>
<tr>
<td>CB</td>
<td>75</td>
<td>25</td>
<td>0</td>
<td>Cobble-Boulder</td>
<td>Basalt wall with projecting pillows</td>
</tr>
<tr>
<td>SB</td>
<td>75</td>
<td>0</td>
<td>25</td>
<td>Sediment-Boulder</td>
<td>Pillow basalts exhibiting chilling cracks with sediments</td>
</tr>
<tr>
<td>BCS</td>
<td>25</td>
<td>25</td>
<td>50</td>
<td>Boulder-Cobble-Sediment</td>
<td>Pillow/ basalt blocks with sediments on a gradual slope</td>
</tr>
<tr>
<td>C</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>Cobble</td>
<td>Talus or broken pillow basalt fragments at the base of a scarp or small hillock. This suggests tectonic activity</td>
</tr>
<tr>
<td>CS</td>
<td>0</td>
<td>25</td>
<td>75</td>
<td>Cobble-Sediment</td>
<td>Exposures of basalts in thick sediment covered plain</td>
</tr>
<tr>
<td>BS</td>
<td>25</td>
<td>0</td>
<td>75</td>
<td>Boulder-Sediment</td>
<td>Sedimented base of basalt wall</td>
</tr>
<tr>
<td>S</td>
<td>0</td>
<td>0</td>
<td>100</td>
<td>Sediment</td>
<td>Sediments</td>
</tr>
</tbody>
</table>


Table 3. Abundance range (mean± SD) of benthic megafaunal groups per km² area in the Carlsberg Ridge area.

<table>
<thead>
<tr>
<th>Faunal groups</th>
<th>Geophysical settings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Off-axial highs (n=2)</td>
</tr>
<tr>
<td>Porifera</td>
<td>8-23 (15.5±10.6)</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>37-125 (81±62.2)</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>11-18 (14.5±4.9)</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>0</td>
</tr>
<tr>
<td>Chordata</td>
<td>4-5 (4.5±0.7)</td>
</tr>
<tr>
<td>Others (Annelidea and Xenophyophora)</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 1. Transect locations of the study area: Shallower transects TVG 2 & 3 and deeper transects TVG 1 & OFOS 1 located in the northern segments; other all deeper transects TVG 4, 5, 6, 7, 8 and OFOS 2 & 3 located in the southern segments in the Carlsberg Ridge.
Figure 2. Representative photographs of each substratum type and their distribution pattern along the transects in the study area.
Figure 3. Megafaunal density and number of taxa along the Carlsberg Ridge with different depths and geophysical settings.
Figure 4. Cluster analysis of substratum types at each transect along the CR.
Figure 5: Cluster analysis of megafaunal assemblages at each transect along the CR.
Figure 6. Underwater images of benthic megafauna along the Carlsberg Ridge.

Shallower: a. Isididae sp1; b. Isididae sp2; c. Brisingidae sp2; 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 sp1; n. Brisingidae sp1; o. Anguilliformes sp2; p. *Cerataspis* sp