First quantitative exploration of benthic megafaunal assemblages on mid oceanic ridge 1 2 system of Carlsberg Ridge, Indian Ocean Sabvasachi Sautva^{1*}, Baban Ingole¹, Daniel O. B. Jones², Durbar Ray¹, K.A. KameshRaju¹ 3 ^{1*}National Institute of Oceanography (CSIR), Regeinal Centre, Mumbai-400053, India 4 ¹National Institute of Oceanography (CSIR), Dona Paula, Goa-403004, India 5 ²National Oceanography Centre, University of Southampton Waterfront Campus, European 6 7 Way, Southampton, SO14 3ZH, UK 8 *Corresponding author sautya@nio.org 9 10 Published in 2017 in the Journal of the Marine Biological Association of the United Kingdom: 11 Sautya, S., Ingole, B., Jones, D.O.B., Ray, D., Kameshraju, K.A., 2017. First quantitative exploration of 12 benthic megafaunal assemblages on the mid-oceanic ridge system of the Carlsberg Ridge, Indian Ocean. 13 Journal of the Marine Biological Association of the United Kingdom 97 (2), 409-417. 14 DOI:10.1017/S0025315416000515 15 16 Abstract 17 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 18 community structure of the Indian Ocean MOR at the Carlsberg Ridge (CR) using 19 20 underwater video observation by the Television Gripper (TVG) and Ocean Floor Observation 21 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 22 23 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 24 greatest in the deeper areas of the CR region, with substrata varying from fine sediments to 25 basalts. A total of 8 substratum types and 90 megafaunal taxa, representing 7 phyla, were 26 identified have been classified throughout the eleven transects. Faunal abundances ranged 27 between 171.3 to 5.7 animals Per 1000 m⁻², with higher abundances at the shallower transect 28 29 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 30 31 frequently encountered faunal components were poriferans and chordates, observed at 32 shallower as well as deeper transects. This is the first detailed investigation of megafaunal 33 assemblages from the Indian Ocean MOR. 34 Keywords: Benthic megafauna; habitat heterogeneity; deep-sea; mid-oceanic ridges; 35 Carlsberg Ridge; Indian Ocean. 36 37 38 39 40 41

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., 2008) 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

- 1 TVG system had similar capacity to OFOS and had two video cameras (1xDSPLMSC 2000
- 2 colour, and 1xOSPREY OE 1390 monochrome digital video), lighting (4xROS QL 3000) and
- 3 telemetry. All the still photographs and video images were collected on digital versatile disc
- 4 (DVD) at the surface. TVG was towed along the predefined track at the speed of about 0.5 to
- 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
- 7 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
- 17 identified based on seabed morphology and composition, such as rock type and sediment
- nature (Figure 2; Table 2).
- 19 The substratum type, presence and identity of all organisms was recorded along each transect.
- 20 Positional information for each photograph was obtained from the navigation data. After
- 21 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
- 25 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
- 27 following equation:
- Width of transect, $W = 2 \times \tan{(\alpha/2)} \times \text{camera altitude } (H)$. Where, α is angle of focal length
- 29 (20°) of the camera.
- The area coverage of each transect was estimated from the total length (L) and width (W) as
- 31 follows: Area $(A) = L \times W$
- Based on the area calculated and after recording the individuals on the entire track, we
- 33 estimated the faunal density at each transect.

Statistical analysis

1 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

14 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, 2 representing 7 phyla, were observed in the underwater video and still images in the two 3 segments of the CR (Table 1; Suppl. Table 1). The population density varied between 5.68 4 and 171.34 animals 1000 m⁻² with a mean of 37.98 \pm 3.31 animals 1000 m⁻² in the study area 5 (Figure 3). 272 of individuals were seen on an off-axial high observed in the shallower 6 7 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 8 deeper transects. Density varied from 60.81 to 171.34 animals 1000 m⁻² (mean 116.07 \pm 9 55.26) in the shallower transects and from 53.53 to 5.68 animals 1000 m⁻² (mean 20.63 \pm 10 15.98) in the deeper transects. The highest density was observed along off axial highs transect 11 of TVG 3, while the lowest was at rift valley wall transect OFOS 3 which was the deepest 12 transect of the study area. Number of taxon recorded from each transect shown in Figure 3. 13 On average the megafaunal assemblage was dominated by cnidarians followed by poriferans 14 15 and echinoderms. The cnidarians were mostly observed in shallower transects located in offaxial highs (Table 3). In both shallow transects the cnidarians were predominantly a black 16 coral, Stichopathes sp. and the substratum type was mostly basalt blocks with cobbles and 17 18 sediments (BCS). In contrast, the deeper transects contained a maximum of six megafaunal groups and were dominated by echinoderms followed by arthropods poriferans, Chordatas, 19 20 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 21 22 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) 23 24 rich areas. Other megafaunal groups, such as xenophyophores and Annelida, were 25 occasionally observed in both the segments.

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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 1
- 2 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). 3
- The sites formed three distinct groups when analysed in terms of their megafaunal similarity 4
- (Figure 5). The multivariate analysis made a clear distinction between the shallow and the 5
- deep areas (<5% similarity from cluster analysis). One group (Group A) comprised the 6
- shallower transects (TVG 2 & TVG 3) and the deeper transects OFOS 2 & 3 located in rift 7
- valley wall and TVG 5, 6, 7 & 8 in rift valley floor made Group B and Group C. Overall 8
- Stichopathes sp., Brisingidae sp2, Isididae sp1, Actinaria sp3 and Hexactinellida sp9 (Figure 9
- 10 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 11
- 12 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 13
- 14 transects OFOS 2 & 3 owing to similarities in density of *Plesiopenaeus* sp, Elpidiidae sp1
- and Enypniastes exima (contributed to 89% similarity). OFOS 1, TVG 1and TVG4 were the 15
- 16 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 17
- period (35 minutes). 18

19 **DISCUSSION**

- All transects observed had basalts present. Some observations, for example the C substratum 21
- types, included talus or broken pillow basal fragments at the base of small mounds, which 22
- may suggest tectonic activity at the area. Multi-beam mapping of the Carlsberg Ridge 23
- between 62°20 E and 66°20 E (KameshRaju et al., 2008) revealed rugged topography with 24
- steep valley walls, structures such as ridge-parallel topographic fabric and axial volcanic 25
- ridges, which correspond with features observed here. In this study, some substrata, such as 26
- sediments (S) and exposed basalts in thick sediment covered plain (CS), were mostly covered 27
- with pelagic sediments, reworked by benthic fauna (such as observed at transect TVG7). 28
- 29 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-30
- Atlantic Ridge (Bell et al., 2013). The general morphology of the Carlsberg Ridge sections 31
- used in the present study is similar to the Mid Atlantic Ridge (MAR) between the Kane and 32
- 33 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).

CONSERVATION ATTENTION

- 1 In the present study 90 taxa were recorded, although most of them were not identified to
- 2 species level, it would seem likely that some of these may be new to science. In dredge
- 3 samples collected at the Carlsberg Ridge in 2009 a new genus and species of hexactinellid
- 4 sponge was discovered (Sautya et al., 2011). In the southern South Atlantic MAR system (see
- 5 Polar Biology, 2006: 29, special issue) benthic diversity was much higher than previously
- 6 recorded for the area especially for echinoderms, molluscs, cheilostome bryozoans and
- 7 amphipods and many of these records were new to the science. About 10% of species in
- 8 MAR-ECO epibenthic invertebrate collections, made in the northern MAR, appeared to be
- 9 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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- 2 Alt C.H.S., Rogacheva A., Boorman B., Hughes J.A., Billett D.S.M., Gooday A.J. and
- Jones D.O.B. (2013). Trawled megafaunal invertebrate assemblages from bathyal
- depth of the Mid-Atlantic Ridge (48°-54°N). *Deep-Sea Research II* 98, 326-340.
- 5 Bell, J.B., Jones, D.O.B., Alt, C.H.S. (2013). Lebensspuren of the Bathyal Mid-Atlantic
- 6 Ridge. Deep Sea Research II 98, 341-351.
- 7 Bergstad O.A., Falkenhaug T., Astthorsson O.S., Byrkjedal I., Gebruk A.V., Piatkowski
- 8 U., Priede, I.G., Santos R.S., Vecchione M., Lorance P. and Gordon J.D.M.
- 9 (2008). Towards improved understanding of the diversity and abundance patterns of
- the mid-ocean ridge macro- and megafauna. *Deep-Sea Research II* 55, 1-5.
- 11 Bergstad O.A. and Godø O.R. (2003). The pilot project "Patterns and process of the
- ecosystems of northern Mid-Atlantic": aims, strategy and status. Oceanologica Acta
- 13 25, 219-226.
- 14 Carney R.S. (2005). Zonation of deep biota on continental margins. Oceanography and
- 15 *Marine Biology an Annual Review* 43, 211-278.
- 16 Clark M.R., Rowden A.A., Schlacher T., Williams A., Consalvey M., Stocks K.I, Rogers
- A.D., O'Hara T.D., White M., Shank T.M. and Hall-Spencer J.M. (2010). The
- ecology of seamounts: Structure, function and human impacts. Annual Review of
- 19 *Marine Science* 2, 253-278.
- 20 Clarke K.R., Gorley R.N. (2006). Primer. Primer-E, Plymouth.
- Felley J.D., Vecchione M. and Wilson Jr. R. R. (2008). Small-scale distribution of deep-
- sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the
- 23 Mid-Atlantic Ridge. *Deep-Sea Research II* 55, 153-160.
- **Fowler C.M.R. and Tunnicliffe V.** (1997). Hydrothermal vent communities and plate
- 25 tectonics. *Endeavour* 21, 164-168.
- Gamo T., Chiba H., Yamanaka T., Okudaira T., Hashimoto J., Tsuchida S., Ishibashi
- J., Kataoka S., Tsunogai U., Okamura K., Sano Y. and Shinjo R. (2001).
- 28 Chemical characteristics of newly discovered black smoker fluids and associated
- 29 hydrothermal plumes at the Rodriguez Triple Junction, Central Indian Ridge. *Earth*
- *and Planetary Science Letters* 193, 371–379.
- 31 Garrison T. (1993). Oceanography: An invitation to Marine Science. Belmont, California:
- Wadsworth. 608 pp.

- 1 Glasby G.P. (1971). Distribution of manganese nodules and Lebensspuren in underwater
- photographs from the Carlsberg Ridge, Indian Ocean. New Zealand Journal of
- 3 *Geology and Geophysics* 16, 1-17.
- 4 Gray J.S. (1974). Animal- sediment relationships. Oceanography and Marine Biology an
- 5 *Annual Review* 12, 263–300.
- 6 Hashimoto J., Ohta S., Gamo T., Chiba H., Yamaguchi T., Tsuchida S., Okudaira S.,
- Watabe H., Yamanaka T. and Kitazawa M. (2001). First hydrothermal vent
- 8 communities from the Indian Ocean discovered. *Zoological Science* 18, 717–721.
- 9 Hogg M.M., Tendal O.S., Conway K.W., Pomponi S.A., van Soest R.W.M., Gutt J.,
- 10 Krautter M. and Roberts J.M. (2010). Deep-sea Sponge Grounds: Reservoirs of
- Biodiversity. UNEP-WCMC Biodiversity Series No. 32.UNEP-WCMC, Cambridge,
- 12 UK.
- 13 KameshRaju K.A., Chaubey A.K., Amarnath D. and Mudholkar A.V. (2008).
- Morphotectonics of the Carlsberg Ridge between 62°20′ and 66°20′ E, northwest
- 15 Indian Ocean. *Marine Geology* 252, 120–128.
- Laughton A.S. (1967). Underwater photography of the Carlsberg Ridge. In Hersey J.B. (eds)
- 17 Deep-sea photography, pp. 191-206. The John Hopkins Press: Baltimore. 310 pp.
- Lutz M.J., Caldeira K., Dunbar R.B. and Behrenfeld M.J. (2007). Seasonal rhythms of
- 19 net primary production and particulate organic carbon flux to depth describe the
- 20 efficiency of biological pump in the global ocean. Journal of Geophysical Research:
- 21 *Oceans* 112 (C10), DOI: 10.1029/2006JC003706.
- 22 **McIntyre A.D.** (2010). Life in the world's oceans: diversity, distribution and abundance.
- Oxford, Blackwell Publishing Ltd.
- McKenzie D.P., Molna, P. and Davie, D. (1970). Plate tectonics of the Red Sea and East
- 25 Africa. *Nature* 226, 243-248.
- 26 Molodtsova T.N. (2013). Deep-sea mushroom soft corals (Octocorallia: Alcyonacea:
- 27 Alcyoniidae) of the Northern Mid-Atlantic Ridge. Marine Biology Research 9, 488-
- 28 515.
- 29 Murton J.B., Baker E.T., Sands C.M. and German C.R. (2003). Detection of an unusual
- large hydrothermal event plume above the slow spreading Carlsberg Ridge, NW
- 31 Indian Ocean. *Geophysical Research Letters* 33, 1-5.

- 1 **O'Hara T.** (2008). Bioregionalisation of the waters around Lord Howe and Norfolk Islands
- 2 using brittle stars (Echinodermata: Ophiuroidea), Department of the Environment,
- Water, Heritage and the Arts. 54pp.
- 4 Ray D., KameshRaju K.A., Baker E.T., Rao A.S., Mudholkar A.V., Lupton J.E.,
- 5 **Prakash L.S., Gawas R.B. and Kumar T.V.** (2012). Hydrothermal plumes over the
- 6 Carlsberg Ridge, Indian Ocean. Geochemistry Geophysics Geosystems 13, 1-15,
- 7 Q01009.
- 8 Ray D., Mirza I.H., Prakash L.S., Kaisary S., Sarma Y.V.B., Rao B.R., Somayajulu
- 9 Y.K., Drolia R.K. and KameshRaju K.A. (2008). Water-column geochemical
- anomalies associated with the remnants of a mega plume: A case study after CR-2003
- hydrothermal event in Carlsberg Ridge, NW Indian Ocean. *Current Science* 95, 355-
- 12 360.
- 13 Rice A.L., Thurston M.H. and New A.L. (1990). Dense aggregations of a hexactinellid
- sponge, *Pheronema carpenteri*, in the Porcupine Seabight (northeast Atlantic Ocean),
- and possible causes. *Progress in Oceanography* 24, 179–196.
- 16 Rowe G.T., Keller G., Edgerton H., Staresinic N. and MacIlvaine J. (1974). Time-lapse
- photography of the biological reworking of sediment in the Hudson Canyon. *Journal*
- of Sedimentary Petrology 44, 549–552.
- 19 Sautya S., Tabachnick K.R. and Ingole B. (2011). A new genus and species of deep-sea
- 20 glass sponge (Porifera, Hexactinellida, Aulocalycidae) from the Indian Ocean.
- 21 Zookeys 136, 13-21.
- Van Dover Cl L., Humphris S.E., Fornari D., Cavanaugh C.M., Collier R., Goffredi
- S.K., Hashimoto J., Lilley M.D., Reysenbach A.L., Shank T.M., Von Damm
- K.L., Banta A., Gallant R.M., Götz D., Green D., Hall J., Harmer T.L., Hurtado
- L.A., Johnson P., McKiness Z.P., Meredith C., Olson E., Pan I.L., Turnipseed
- M., Won Y., Young III C.R. and Vrijenhoek R.C. (2001). Biogeography and
- ecological setting of Indian Ocean hydrothermal vents. *Science* 294, 818-823.
- Van Dover C.L. (2000). The ecology of deep-sea hydrothermal vents. *Princeton University*
- 29 Press, Princeton N. J. 352 pp.
- Vecchione M., Bergstad O.A., Byrkjedal I., Falkenhaug T., Gebruk A.V., Godø O.R.,
- Gislason A., Heino M., Høines Å.S., Menezes G.M.M., Piatkowski U., Priede I.G.,
- 32 Skov H., Søiland H., Sutton T. and Wenneck T.L. (2010). Biodiversity patterns and
- process on the mid-Atlantic ridge. In McIntyre A. (eds) Life in the world's oceans:

1	diversity, distribution and abundance. pp. 103-121. Oxford, Blackwell Publishing
2	Ltd. 384pp.
3	Williams A., Althaus F., Dunstan P.K., Poore G.C.B., Bax N.J., Kloser R.J. and
4	McEnnulty F.J. (2010). Scales of habitat heterogeneity and megabenthos
5	biodiversity on an extensive Australian continental margin (100-1,100 m depths).
6	Marine Ecology 31, 222-236.
7	

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

Station ID		Start Location		End Location		Depth range (m)	Bottom temperature	Transect length (km)	Area covered	Total number of individuals
	Date	Latitude (N)	Longitude (E)	Latitude (N)	Longitude (E)	, ,	(°C) (* CTD failed)		(km^2)	observed
					Sh	allower				
	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
TVG3	25/10/2007	05°26.452'	61°26.578'	05°26.684'	61°26.459'	1834 - 1656	*	0.619	0.6537	114
					D	eeper				
	Rift valley floor	r								
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
TVG4*	03-	03°58.505'	63°01.000	03°58.556'	63°01.041'	3558-3365	1.90	0.201	0.2034	2
	04/11/2007									
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
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
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
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
	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
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
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

^{*} 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.

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

Table 3. Abundance range (mean± SD) of benthic megafaunal groups per km² 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)				



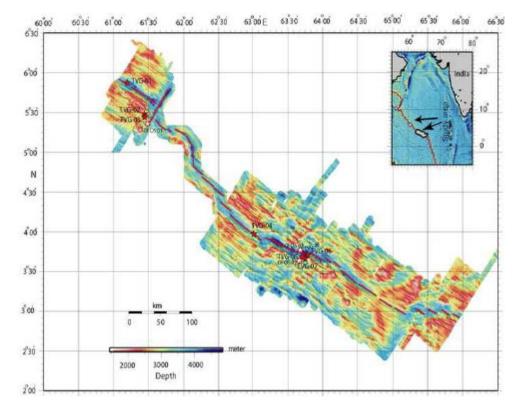


Figure 1. Transect locations of the study area: Shallower transects TVG 2 & 3 and deeper transects TVG 1 & OFOS 1 located in the northern segments; other all deeper transects TVG 4, 5, 6, 7, 8 and OFOS 2 & 3 located in the southern segments in the Carlsberg Ridge.

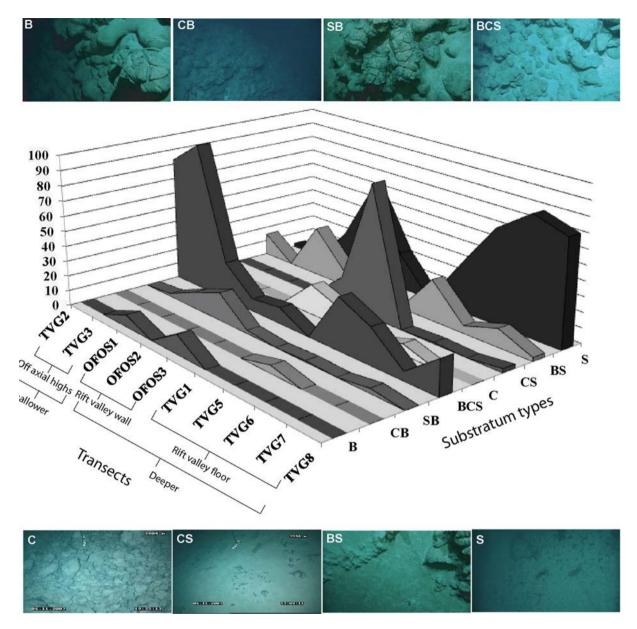


Figure 2. Representative photographs of each substratum type and their distribution pattern along the transects in the study area

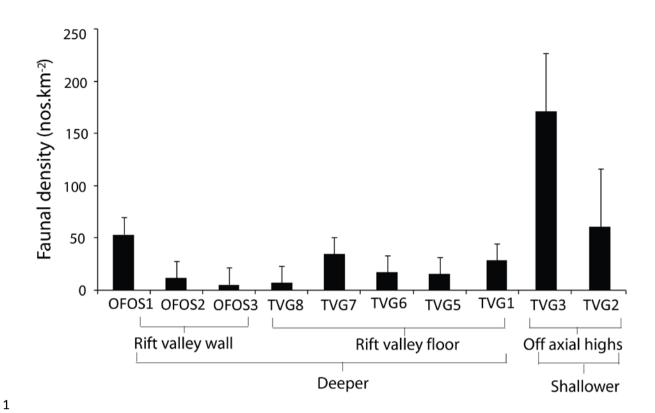
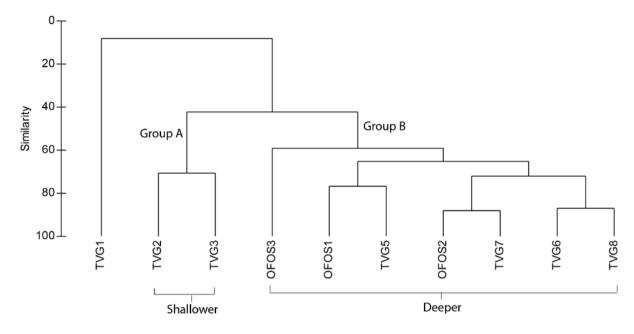
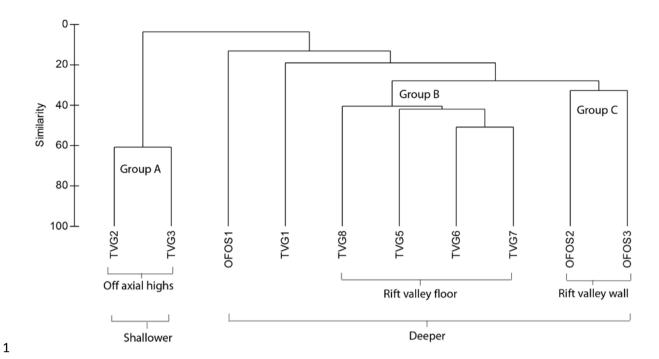


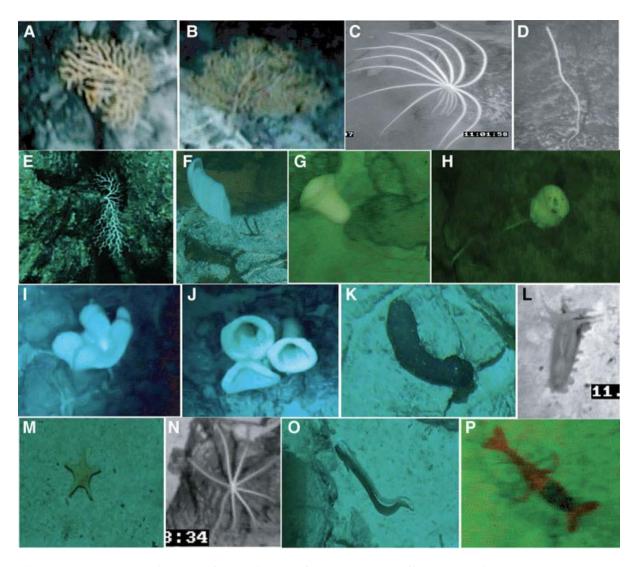
Figure 3. Megafaunal density and number of taxa along the Carlsberg Ridge with different depths and geophysical settings



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



2 Figure 5: Cluster analysis of megafaunal assemblages at each transect along the CR.



2 Figure 6. Underwater images of benthic megafauna along the Carlsberg Ridge.

- 3 Shallower: a. Isididae sp1; b. Isididae sp2; c. Brisingidae sp2; d. Stichopathes sp;
- 4 Deeper: e. Stylasterine sp; f. Aulocalycidae glass sponge; g. Hyalonema sp; h. Bolosominae sponge; i.
- 5 Crateromorpha sp; j. Rossellidae glass sponge; k. Benthodytes sp; l. Peniagone sp; m. Asteroid sp1;
- 6 n. Brisingidae sp1; o. Anguilliformes sp2; p. Cerataspis sp

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