

Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin.

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Abstract.

The Arabian Sea oxygen minimum zone (OMZ) impinges upon the Indian continental margin OMZ at bathyal depths (100-1500m) resulting in changes in oxygen availability and sediment geochemistry. Between September and November 2008, a multi-national research expedition visited this region to test how long-term hypoxia the structure of sea floor ecosystems and their role in marine biogeochemical cycles. Video surveys were conducted by the submersible Shinkai 6500, in order to quantify changes in the epi-benthic megafaunal and lebensspuren (biogenic trace) assemblages at six stations, spanning the OMZ (540 – 2000m water depth). Megafaunal abundance and community structure changed across the OMZ, with total abundance observed to correlate with the quality of sediment organic matter (C: N ratio). Taxonomic diversity and lebensspuren complexity increase concomitantly with the depth dependent oxygen gradient. With the exception of the fishes, epibenthic megafauna were absent in the OMZ core (540m; $[O_2] \approx 0.35 \mu\text{M}$). Peaks in megafaunal abundance were observed at 800m ($[O_2] \approx 2.09 - 2.63 \mu\text{M}$), characterised by high densities of Ophiuroids ($0.2073 - 0.4430 \text{ ind.m}^{-2}$) and Decapods ($0.1158-0.1480 \text{ ind.m}^{-2}$). Frame grabs taken from the video footage were used to measure the size of individual ophiuroids and decapods, allowing the first estimation of megafaunal carbon demand across an OMZ. Carbon demand by these numerically abundant taxa ranged between $3.374 - 56.420 \text{ mmol C. m}^{-2} \cdot \text{d}^{-1}$. This exceeds the estimated rate of organic matter remineralisation for the infaunal community made at similar depths on the Pakistan margin ($1.918 - 39.319 \text{ mmol C. m}^{-2} \cdot \text{d}^{-1}$ (Woulds, *et al.*, 2009), demonstrating the importance of the megafauna in benthic ecosystem function, within an oxygen minimum zone.

Key Words.

Arabian Sea; Carbon Demand; Lebensspuren; Megafauna; Oxygen Minimum Zone; Video Survey

1. Introduction.

Oxygen minimum zones (OMZs) are important features structuring the marine environment at the continental margins (Gooday, *et al.*, 2010). Defined as discrete water bodies where dissolved oxygen levels are persistently below 0.5 ml.l^{-1} ($22 \text{ }\mu\text{M}$) (Levin 2003), OMZs form in mid-water and persist over geological time periods as a consequence of high primary productivity at the oceans surface combined with a stratified water column. This generates an isolated water body where organic matter flux is high and biological oxygen demand exceeds the supply of oxygen into the water column (Wyrki 1962; Olson, *et al.*, 1993) Although they form in the water column, the effects of an OMZ are acutely experienced at the sea floor, where strong gradients in both oxygen availability and organic matter flux are observed (Devol and Hartnett 2001). At present, approximately 6 % of the continental margins (1.5 million km^2 of seafloor) experience permanent dysoxic conditions (Helly and Levin 2004) within oxygen minimum zones. This area is predicted to grow as a consequence of both anthropogenic changes in climate and ecosystem dynamics (Bakun and Weeks 2004; Stramma, *et al.*, 2008).

The Arabian Sea oxygen minimum zone impinges upon $285,000 \text{ km}^2$ of continental margin sea floor (Helly and Levin 2004), between 100 – 1500 m water depth (Schulz, *et al.* 1996; Cowie, *et al.* 1999; Gooday, *et al.* 2009). As in most benthic ecosystems, energy inputs to the oxygen minimum zone sea floor are primarily from primary production at the sea surface (Graf 1992). The sediment within this region is characterised by a high organic carbon content (Schulz, *et al.*, 1996; Cowie, *et al.*, 1999; Schulte, *et al.*, 2000) and the preservation of highly labile organic compounds, such as amino acids (Vandewiele, *et al.*, 2009), lipids (Schulte, *et al.*, 2000; Jeffreys, *et al.*, 2009b) and photosynthetic pigments (Shankle, *et al.* 2002; Woulds and Cowie 2009). Thus, the benthic environment within an oxygen minimum zone is both food rich and oxygen deficient. These eutrophic conditions are not uniform and oxygen concentrations change along a depth gradient as the influence of the OMZ weakens. This produces a zonation pattern at the sea floor which includes an anoxic region, at the OMZ core, and boundary regions where there is a transition in ambient oxygen correlated to depth and tidal cycles (Cowie and Levin 2009; Gooday, *et al.*, 2009). In consequence, the benthic community changes along the depth-dependent oxygen gradient, with bacteria (Schmaljohann, 2001; Schmaljohann, *et al.*, 2001; Ulloa, *et al.*, 2006; Stevens and Ulloa 2008) and calcareous foraminifera dominant at the OMZ core (den Dulk, et al 1998; Gooday, et al 2000; Kurbjeweit, et al 2000; Schumacher, et al 2007) and high densities of hypoxia tolerant foraminiferans and metazoans

characterising the boundary regions (Wishner, *et al.*, 1990; 1995; Levin, *et al.*, 1991; Cook, *et al.*, 2000; Goody, *et al.*, 2000; 2009; Murty, *et al.*, 2009).

The epi-benthic megafauna (>1 cm in size) are defined as the animals occupying the sediment surface, which are large enough to be observable within a photograph or video image (Grassle, *et al.*, 1975; Gage and Tyler 1991). These organisms are the most conspicuous component of the sea floor community, but are relatively poorly studied. The presence of benthic megafauna has been described within oxygen minimum zones of the Chilean continental margin (Quiroga, *et al.*, 2009; Sellanes, *et al.*, 2010), on the slope of an Eastern Pacific seamount, Volcano 7 (Wishner, *et al.*, 1990; 1995; Levin, *et al.*, 1991), and in the Arabian Sea; at the Pakistan (Murty, *et al.*, 2009) and Oman (Smallwood, *et al.*, 1999) continental margins. These studies report the presence of high densities of specific megafaunal taxa, such as Ophiuroids and Decapod crustaceans, at the boundaries of an oxygen minimum zone. However, fishes were the sole megafauna present in the OMZ core, where oxygen concentrations were lowest. The megafauna exhibit a zonation, with peaks in abundance and diversity observed along the boundaries of OMZs, both in the Arabian Sea (Smallwood, *et al.*, 1999; Murty, *et al.*, 2009) and eastern Pacific Ocean (Wishner, *et al.*, 1990; 1995; Sellanes, *et al.*, 2010). All of which suggests the role of “edge-effects,” where low oxygen, food rich conditions at the boundaries of an OMZ are exploited by high densities of hypoxia tolerant megafauna (Levin, 2003).

In deep-sea environments, benthic megafauna occurrence is often spatially patchy (Bluhm, 2001a; 2001b; Piepenburg, *et al.*, 1995; 1996; 1997; Williams, *et al.*, 2009; Howell, 2010). Where megafauna are abundant they contribute significantly to benthic community biomass (Smith and Hamilton, 1983; Lampitt, *et al.*, 1986; Smith 1992; Thurston, *et al.* 1994), oxygen consumption (Piepenburg, *et al.*, 1995) and carbon demand (Tyler, *et al.*, 1993; Ambrose, *et al.*, 2001; Christiansen, *et al.*, 2001; Renaud, *et al.*, 2007). In addition, dense aggregations of megafauna play an important role in structuring the marine benthos, by physical disturbance of the sediment (Gallucci, *et al.*, 2008), predation upon meio- and macrofaunal assemblages (Ambrose. 1993; Hudson and Wigham 2003), and by selectively removing labile organic matter from the sediment (Miller, *et al.*, 2000; Ginger, *et al.*, 2001). Within an oxygen minimum zone the megafauna have been observed feeding at multiple trophic levels (Jeffreys, *et al.*, 2009a), which control both the quantity and quality of organic matter within deep sea sediments (Smallwood, *et al.*, 1999; Jeffreys, *et al.*, 2009b). As such, shifts in megafaunal zonation across an oxygen minimum zone may act as predictors of important biogeochemical processes, such as organic matter recycling and burial.

Lebensspuren are the conspicuous traces left by both in- and epibenthic megafauna organisms at the seafloor (Kitchell, *et al.*, 1978; Kitchell 1979; Wheatcroft, *et al.*, 1989). In the deep-sea, these traces can persist over long time periods, with their densities directly controlled by faunal reworking of the sediments (Young, *et al.*, 1985; Gaillard, 1991). As such, they provide an effective predictor of bioturbation intensity, which is consistent with both megafaunal abundance and radioactive lead (^{210}Pb) and thallium (^{234}Th) derived bioturbation profiles (Turnewitsch, *et al.*, 2000). Whilst not all taxa leave traces at the sea floor (Kaufmann and Smith, 1997), infaunal megafauna, such as enteropneusts (Mauviel, *et al.*, 1987) and Echiurans (Ohta, 1984), may often only be observed via the traces they leave behind. Therefore, whilst caution is required in interpreting lebensspuren data, when considered alongside megafaunal abundance and biomass (e.g. Jones *et al.*, 2007a) they provide valuable information upon megafaunal activity and the presence of a megafaunal assemblage within the sediment.

Photographic surveys provide an effective method of investigating the spatial distribution and abundance of deep-sea fauna (Solan, *et al.*, 2003) and lebensspuren. However, spatial heterogeneity of megafaunal assemblages tends to negatively bias abundance estimates derived from photo-transect surveys. By providing images continuously over time, video survey techniques mitigate against this problem and produce density estimates comparable with direct visual census of an area (Tessier, *et al.*, 2005). Still-images can subsequently be captured from the video allowing the size of individual organisms to be measured, from which valuable ecological data such as the biomass and respiratory demand for both oxygen and carbon can be derived (Christiansen and Thiel, 1992; Christiansen, *et al.*, 2001; Bluhm, *et al.*, 1995; Piepenburg, *et al.*, 1995; 1997).

The present study is the first description of the megafaunal assemblage across the little explored Indian continental margin of the Arabian Sea. This region is impacted by the Arabian Sea OMZ between 200 and 1500 m. The present study describes the zonation in fauna between six sites spanning the OMZ from 540m to 2000 m. The study used video survey techniques to quantify and compares the megafaunal abundance, taxonomic diversity and the presence of lebensspuren, across the OMZ. In addition, the study used frame-grab images to measure the sizes of individuals from key megafaunal taxa, and thus obtain estimates of biomass. The aim of the present study is to investigate the hypothesis that both megafaunal abundance and assemblage structure change across the Indian margin OMZ, correlated to the changes in the ambient oxygen availability and sediment organic matter content. Assemblage structure was investigated at multiple spatial scales (Magurran, 2004) by describing changes megafaunal assemblage composition, testing differences in both taxonomic

diversity and testing difference in the abundance of key taxa, across the OMZ. The study also presents the first estimates of physiological carbon demand by megafaunal taxa across an oxygen minimum zone, derived from the estimated biomass and published metabolic rates of individual taxa; and demonstrated that changes in megafaunal assemblage will ultimately influence the rate of organic matter turnover.

2. Materials & Methods

Between September and November 2008, a multi-national research expedition to the Arabian Sea oxygen minimum zone at the Indian continental margin, took place aboard the R/V Yokosuka (YK08-11). The submersible Shinkai 6500 made a total of 24 dives at six stations, along two transects spanning the Arabian Sea oxygen minimum zone, at the Indian continental margin (Fig. 1). Each dive was recorded using the Shinkai 6500's camera system, which provided 140 hours of video footage of the sea floor. Approximately 2 % of the footage was deemed suitable for use in quantitative video surveys, from which 95 minutes of video footage was used within 19 distinct visual surveys.

2.1 Environmental Data

Ambient salinity, temperature and pressure were recorded by Shinkai 6500 using a CTD (Conductivity-Temperature-Depth) array. Ambient oxygen concentrations were measured at each station using an Aanderra optode mounted upon the submersible. CCOptode calibration proceeded by Winkler Titration against nitrogen bubbling fresh water, and the accuracy of the instrument was assumed to be $\pm 1 \mu\text{M}$ at oxygen concentrations $< 50 \mu\text{M}$ (A. Tengberg, *pers. comm.*) These data are summarised to provide an overview of the background environmental conditions within the study area (Fig. 2).

Sediment samples, collected as push cores, were collected at each station by Shinkai 6500. Three 8.2 cm diameter push cores were obtained from each station with the exception of T1 1100m, where only one core could be obtained. Sediment samples, from the surficial 1 cm, were homogenized and deep-frozen at $-80 \text{ }^\circ\text{C}$ until they could be further processed. Sediment samples were sub-sampled whilst frozen using a geology hammer to remove a 5 g aliquot of frozen sediment. Sediment sub-samples were lyophilised, and porosity determined based upon the change in volume and mass of the sediment (Breitzke, 2006). Sediments were acidified to remove inorganic carbon by addition of excess 1 mol.l^{-1} hydrochloric acid, and incubation at $30 \text{ }^\circ\text{C}$, for 24 hours in an acid fumed environment (Hedges and Stern, 1984). Acidified sediments were dried to constant weight at $60 \text{ }^\circ\text{C}$

and the total organic carbon content (% TOC) and total nitrogen content (% TN) determined using an ANCA-GSL elemental analyser. These results were used to calculate a C: N ratio for each sediment sample. In the present study, the C: N ratio provides a crude proxy of sediment organic matter quality, based upon the departure of a given sample from the Redfield Ratio of 6.6 (e.g. Hedges and Keil, 1995).

2.2 Video Survey Technique

Video footage was recorded during seven dives, at the six survey stations (Table 1). This footage was used to carry out a quantitative visual survey of megafaunal assemblage, and note the densities of any conspicuous lebensspuren. Surveys were conducted using a video census protocol derived from the belt transect technique proposed by Brock (1954), where the width of the survey area was defined by the field of view of the camera.

Independent replicate video surveys were carried out at each station to quantify abundance of the megafauna and lebensspuren. Each survey consisted of five one minute counts spread across a 10 minute period. Densities of megafaunal taxa and lebensspuren were recorded in individuals observed per unit time, for every one minute time interval. Densities (ind. min^{-1}) were converted to a relative abundance per unit area (ind. m^{-2}) using the width of the camera field of view and the distance moved by the submersible in one minute.

Frame-grabs were taken from the footage during every minute of surveyed footage. These were used to calculate the width of the camera field of view, using the video imaging software Image-J. Images were calibrated to a 20 cm scale provided by four laser pointers incorporated into the Shinkai 6500 camera system. Abundances

(ind. m^{-2}) were calculated for each one minute count by the following formula:

$$\text{Eq. 1: } D_{\text{area}} = D_{\text{time}} / (W_c * V_{\text{min}})$$

Where D_{area} is the relative abundance per unit area (ind. m^{-2}), D_{time} is the relative abundance per unit time (ind. min^{-1}), W_c is the width seabed in the camera field of view (m) and V_{min} is the average velocity of the submersible ($30.87 \text{ m. min}^{-1}$). Mean abundance values were then calculated over each five or ten minute period, in order to mitigate against the inherent spatial patchiness of the megafaunal assemblage, reducing the inherent variation in the data and providing a more effective measure of relative abundance at each station.

Precision is a major issue within visual surveys (Kimmel, 1985; Sayer and Poonian, 2007), and each replicate within the present study covers a large spatial area. This allows the study to account for the vast spatial heterogeneity reported in deep-sea megafauna (e.g. Piepenberg, *et al.*, 1995; Smallwood, *et al.*, 1999; Renaud, *et al.*, 2007; Murty, *et al.*, 2009). However, the large area within each video survey limits the degree of taxonomic resolution with which the study can be accomplished. This study concentrated on recording the abundance of 15 taxonomic groups (Table 2), within which contributing organisms were further identified using both frame grabs and the present literature on Arabian Sea oxygen minimum zone megafauna (Smallwood, *et al.*, 1999; Jeffreys, *et al.*, 2009a; b; Murty, *et al.*, 2009). Conspicuous lebensspuren were identified and assigned to five groups, following Gaillard's (1991) English-language nomenclature (table 3). At each of the six survey stations, total megafaunal abundance was calculated by aggregating the abundance data for each taxonomic group. The level of variation in the megafaunal assemblage was quantified using the Shannon diversity index (Shannon, 1948), with indices calculated for each replicate visual survey conducted.

2.3 Megafaunal Carbon Demand Estimates

Estimation of biomass and carbon demand was restricted to two numerically abundant taxa the Ophiuroidea and the decapods crustaceans. Decapod measurements were carried out using the most commonly observed crustaceans, the aresteid and solenocerid shrimps (*Plesiopenaeus spp.* & *Solenocera spp.*). Seven hundred and forty frame grabs were captured randomly across the six stations and sorted to remove unsuitable images. Blurred images, images with less than 30 % of the visible seafloor, and images with no visible scale were subsequently removed. The Image-J software package was used to measure the size of visible ophiuroids and decapod crustaceans, calibrated to the laser scale in each image (after Barker, *et al.*, 2001).

Ophiuroid size was measured as disc diameter (cm) for a sample of 86 individual specimens. The biomass of individual ophiuroids was calculated using the size: weight relationship described by Piepenburg & Schmid (1996) and converted to wet weight, based upon a conversion ratio of 12.08 (Gage, 2003). These were combined to generate the following size: weight conversion:

$$\text{Eq. 2: } W_w = (0.1507 \cdot d^{2.488}) / 12.08$$

Where W_w is the wet weight (in grams) and d is the disc diameter in centimetres. Decapod size was measured as carapace length (cm), for a sample of 97 individual specimens. Conversion of decapod

size to wet biomass was conducted using the size: weight conversion ratio described by (Barriga, *et al.*, 2009):

Eq. 3:
$$W_w = 0.00321 \cdot L_c^{2.37026}$$

Where W_w is the wet weight (in grams) and L_c is the Carapace length of a given individual.

From the individual weights calculated, the carbon demand of both the Ophiuroidea and decapods could be estimated at each station in the present study. Biomass per unit area was calculated, at each station for both the Ophiuroidea and Decapoda, as the product of the abundance of each taxon and the median wet weight of an individual. Carbon demand was calculated, based upon mass specific respiration rates of echinoderms and crustaceans of 0.3 and 1.1 mmol O₂ g⁻¹ h⁻¹ respectively (Piepenburg *et al.*, 1995). These were converted to carbon demand, using a 1:1 stoichiometric relationship between respiration and carbon demand and a respiratory coefficient of 0.85 (Smith, 1978; Renaud, *et al.*, 2007). Estimates were restricted to stations where the respective megafaunal taxa were present.

2.4 Data Analysis

Data analysis was conducted in R, using the *stat* (R Development Core Team, 2009), *nlme* (Pinheiro, *et al.*, 2009), *vegan* packages (Oksanen, *et al.*, 2009), alongside the multivariate statistical package PRIMER v5 (Clarke and Warwick, 2001). The data were graphically explored to assess its fit to the required assumptions of homoscedacity (homogeneity of variance) and independence required to conduct parametric statistical tests (Box, 1953; Quinn and Keough, 2002; Zuur, *et al.*, 2010). Graphical data exploration was utilised in place of statistical tests for homoscedacity, e.g. Levene's test, because these tests are ineffective in dealing with small to medium sized datasets (< 25 samples). All data violated the assumptions of homoscedacity which underlie parametric statistics and so analysis preceded using techniques designed to minimise the effect of this violation.

Variation in megafaunal abundance was investigated graphically by Cluster analysis, based upon a Bray-Curtis dissimilarity matrix of the untransformed abundance data. Changes in Lebensspuren abundance between stations were explored by Cluster analysis, based upon a Euclidean distance between each station. These cluster analysis graphically present the variation both within and between the six stations (Clarke, 1993; Quinn and Keough, 2002), providing a proxy for the Beta diversity in both the megafaunal and Lebensspuren assemblages (Magurran, 2004).

Similarity Percentage Analysis (SIMPER) of the Bray-Curtis dissimilarity matrix (Clarke, 1993) was used as an exploratory tool, to identify the main taxonomic groups contributing to megafaunal assemblage structure. SIMPER is a descriptive statistical technique which identifies the taxonomic groups contributing both to the similarity between replicates at each station, and dissimilarity between stations. Differences in the main taxonomic groups, total megafaunal abundance and diversity were subsequently tested between stations using univariate statistical tests.

Differences in abundance and diversity were tested between stations by fitting an analysis of variance model using the generalised least squares (GLS) technique. This method uses log-likelihood estimation to fit a linear model to the data, imposing a specific variance structure (Pinheiro and Bates, 2000). In the present study, variance of each dataset was partitioned between the six survey stations as an exponential function of the response variable. All data were tested for significance, at a level of

$p < 0.05$, with *post-hoc* testing conducted using Bonferroni corrected pair-wise

t-tests. Where a GLS model could not be fitted to the data, differences between stations were tested using the non-parametric Kruskal-Wallis test, with *post-hoc* testing conducted using the method described by Siegel & Castellan (1988).

Differences in estimated carbon demand by the Ophiuroidea and Decapoda were tested between stations. A two-way extension of the GLS model was used to test for differences in carbon demand as a response to the interaction between station and taxonomic group. Variance in carbon demand, as the response variable, was partitioned between both station and taxonomic group, as factorial predictors, mitigating the effects of heterogeneous variance within the model. Data was tested for significance, at $p < 0.05$, and all data graphically investigated to ensure it compliance with model assumptions.

The significance of any changes in lebensspuren were tested, between stations, using a permutational multivariate analysis of variance (perMANOVA), a robust non-parametric statistical technique (Legendre and Anderson, 1999; Anderson, 2001; McArdle and Anderson, 2001). Differences in the relative abundance of the identified Lebensspuren were tested at a significance level of $p < 0.05$, based on 1000 permutations of the Euclidean distance similarity matrix.

Correlation tests were used to investigate potential relationships between megafaunal abundance, diversity and five of the environmental parameters described at each station. Spearman's rank

coefficient (ρ) was used to assess the strength and significance of linear correlations (Spearman, 1904) between abundance and diversity of the megafaunal assemblage; and water depth, ambient oxygen concentration, sediment total organic carbon, total nitrogen and C: N ratio.

3. Results

3.1. Environmental Description

Table 4 provides a summary of the environmental conditions at each of the six survey stations. Oxygen concentrations are strongly correlated with depth across the six station ($\rho = 0.9875$, $p < 0.0001$); increasing from $0.35 \mu\text{M}$ at station T1 540m, to

$107.63 \mu\text{M}$ at T1 2000m. Temperature exhibited a similar trend, with a strong negative correlation with depth observed ($\rho = -0.9754$, $p < 0.0001$). Sediment organic carbon content was highest at 540m, exhibiting a weak negative correlation with depth ($\rho = -0.6650$; $p < 0.0001$). Concentrations of organic carbon and total nitrogen were highest between 800 and 1100m, exhibiting strong correlations with the C: N ratios as a proxy for sediment OM quality (% TOC: $\rho = -0.7568$, $p = 0.0002$; % TN: $\rho = -0.9027$, $p < 0.0001$).

Surficial sediments exhibited high porosity between 540 and 1100 m depth, with the sea floor at stations between these depths was typically homogenous composed of fine grained sediments. At station T1 540m, patches of sea floor were characterised by sharp crested ripples suggesting the action of strong currents upon a relatively stable sediment surface. Likewise at the 800 m stations slight rippling of the sea floor was observed. Surficial sediment at the 2000 m station exhibited the lowest porosity, with the most striking feature of the sediment at this station being heavy bioturbation, evidenced by the high levels of lebensspuren observed. No rocky outcrops were observed to be present, although carbonate deposits were observed at the 1100 m stations. Figure 3 provides a series of images representative of the sea floor at each station.

3.2. Zonation patterns of Lebensspuren.

Lebensspuren exhibited a clear zonation, across the six stations. No traces were observed at stations T1 540m and T1 800m, where oxygen levels were low. However, there is a shift to bioturbated sediments between 800 and 1100 m, with a progressive change in the lebensspuren assemblage (Fig. 4). The stations typically cluster together into four station specific groups. Station T1 1100m appears to be a distinct outlier however, with high variation between the replicate surveys observed. The

lebensspuren assemblage was observed to differ significantly across the Indian margin ($p = 0.0319$; $df = 5$ $F = 3.451$), with station specific differences explaining 57% of the variation in the lebensspuren density ($R^2 = 0.57$).

3.3 Megafaunal Assemblage Structure

The megafaunal assemblage varied across the Indian Margin OMZ (Table 5). At 540m, the megafauna were effectively absent, represented by only one taxonomic group, compared with 2000m where fourteen of the fifteen taxa were observed. Total megafaunal abundance and diversity (Fig. 5) differed significantly across the six stations (Table 6). Total megafaunal abundance was observed to be greatest at 800m, compared with low abundances at both 540 and 2000 m. *Post-hoc* t-tests revealed that the peak in abundance at T1 800m was significantly greater than the abundance levels recorded at either 540 m ($p = 0.018$ $t = 4.120$) or 2000 m ($p = 0.025$ $t = 3.950$), with all other stations falling as intermediates. In contrast taxonomic diversity, measured by the Shannon diversity index, was highest between 1100m and 2000m.

Cluster analysis, based upon a Bray-Curtis dissimilarity index illustrates a clear shift in assemblage variation between the six stations (Fig. 6). This analysis places the six stations into three distinct groups, based upon the dissimilarity of replicate surveys. Replicate surveys conducted at T1 540m clustered together at 90% similarity. Likewise, surveys conducted at T1 2000m clustered together at 50% similarity with one replicate from T1 1100m. The majority of surveys conducted between 800m and 1100m clustered together as a large heterogeneous group, indicating that the megafaunal assemblage was more variable at these stations.

SIMPER analysis was used to investigate which taxonomic groups contributed most to megafaunal assemblage structure. This analysis identified seven taxa which repeatedly contributed to either within station similarity or the differences between stations. The key taxonomic groups identified were the Actinaria; Decapoda; Ophiuroidea; Asteroidea; Holothuria; Echinoidea and the Gnathostomata (fishes). Each group exhibited a significant difference in abundance between the six stations (Table 6), with most groups exhibiting the highest abundance between 800m and 1100m (Fig. 7). The fishes were the only taxa present at the 540m station, where they were found in significantly higher densities than at 2000m (*post-hoc* t-test: $p = 0.0015$, $t = 7.1155$). The 800m stations tended to be characterised by peaks in the abundance of the Ophiuroidea and Decapoda, in contrast to which low densities of Asteroidea and Echinoidea appear to characterise the 1100m stations. Holothurians were observed at only one station, T2 1100m.

Changes in the relative abundance of each taxon were found to correlate with changes in environmental conditions across the OMZ (Table 7). Megafaunal abundances were typically observed to correlate strongly with sediment organic matter concentration (% TOC; % TN) and quality (C: N ratio), suggesting both organic matter availability and characteristics are important predictors of megafaunal abundances. In contrast, both taxonomic diversity and the relative abundances of two taxa, the Asteroidea and Echinoidea, were strongly correlated with oxygen availability. Thus, both oxygen and organic matter availability may act as predictors of megafaunal assemblage structure.

3.4 Megafaunal Carbon Demand.

Estimates of the Ophiuroid and Decapod carbon demand were obtained for five of the six stations. The individual carbon demand of each taxon, is linked both to their specific physiology and relative abundance, reflecting the distribution of each taxon observed across the OMZ (Fig. 8). Highest carbon demand by both Ophiuroids and Decapods is observed at the 800m stations, where they contribute approximately 45 - 50 % of assemblage abundance respectively. A two-way GLS identified a significant interaction between taxonomic group and station ($p = 0.0132$, $df = 4$; $F = 4.1485$), explaining the change in carbon demand across the OMZ. Both station

($p = 0.0052$ $df = 4$; $F = 5.1292$) and taxonomic group ($p < 0.0001$ $df = 1$; $F = 45.863$) were significant predictors of the differences in carbon demand. Therefore, the changes in carbon demand, across the OMZ, reflect both the change in megafaunal abundance and differences in metabolism of the taxonomic groups present.

4. Discussion

Megafaunal assemblage structure changed across the Indian margin oxygen minimum zone, with abundance correlated to sediment organic matter quality and diversity increasing concomitantly with oxygen availability. These results are broadly consistent with previous research, showing depth-dependent zonation of the megafaunal community (Wishner, *et al.*, 1990; 1995; Levin, *et al.*, 1991; Murty, *et al.*, 2009) and high diversity at the edges of an OMZ (Gooday, *et al.*, 2009; 2010; Murty, *et al.*, 2009; Sellanes, *et al.*, 2010). The present study presents the first estimates of megafaunal carbon demand changes within oxygen minimum zone. Although restricted to the Ophiuroidea and Decapoda, these results demonstrate that changes in megafaunal assemblage structure across the OMZ may strongly influence benthic organic matter fluxes, and therefore provide support to the

hypothesis that the megafaunal assemblage can directly control the availability and quality of organic matter within oxygen minimum zone sediments (Smallwood, *et al.*, 1999; Jeffreys, *et al.*, 2009;).

The design of a study to investigate the ecology of deep-sea megafaunal assemblages is technically challenging (Gage and Tyler, 1991). To date, photographic surveys have been considered the most effective method of quantifying deep-sea megafaunal abundance and distribution (Haedrich, *et al.*, 1975; Christiansen and Thiel, 1992; Thurston, *et al.*, 1994; Nybakken, *et al.*, 1998; Hughes and Gage, 2004) as well as estimating size distributions and biomass (e.g. Christiansen, *et al.*, 2001; Renaud, *et al.*, 2007). However, photographic surveys are typically highly sensitive to spatial patchiness within the faunal assemblage, which may introduce significant biases into the data (Lauerma, *et al.*, 1996; Sayer, 2007; Murphy and Jenkins, 2010). Video survey techniques provide an effective alternative to photographic surveys, which make use of the footage obtained from video sledges and trawls, Remotely Operated Vehicles (ROVs) or Submersibles. By providing continuous footage of the survey area, video surveys allow the small scale variations in a faunal assemblage to be controlled within each sampling unit, and when the camera field of view is calibrated correctly the survey can effectively be constrained to a known area. As such, in comparative studies, video-survey techniques estimate faunal abundance with a high degree of accuracy (Tessier, *et al.*, 2005). In the present study, all abundance data were collected using a standardized video census protocol, using the same survey vehicle. During replicate surveys, footage was calibrated at one minute intervals using the laser scale of the Shinkai 6500 camera system to provide a standardized survey technique. This minimized the confounding effects of small scale patchiness within the megafaunal assemblage at each station (e.g. Piepenburg, *et al.*, 1996; Piepenburg and Schmid, 1996; Kaufmann and Smith, 1997; Nybakken, *et al.*, 1998; Jones, *et al.*, 2007a; b), and any effects of the presence of the survey vehicle upon animal behaviour (e.g. Nash, *et al.*, 1984; Sayer and Poonian, 2007).

The study site is impacted by the Arabian Sea OMZ. Within the present study, ambient oxygen concentrations are consistent with those reported by Schulz *et al.* (1996), using Winkler titration calibrated CTD at the Indian and Pakistan margins. These data clearly show intense oxygen depletion at the 540m and 800m stations, with oxygen concentrations exhibiting large increases between 540 & 800 m;

800 & 1100 m; and 1100 & 2000 m. Changes in oxygen concentration across the six stations, follow a depth dependent decrease in ambient temperature and increase in salinity, characteristic of continental margin environments (Levin and Dayton, 2009). In contrast, the geochemical parameters of the surficial sediment do not appear to exhibit any simple linear relationships with depth, across

the six study stations. Organic carbon content (% TOC) was observed to peak at the 540m station but there was considerable lateral variation in organic matter content across the 800m and 1100m stations, where organic matter quality was highest. This indicates that the availability of organic matter and its quality are not directly influenced by oxygen availability (Cowie, *et al.*, 1999; Vandewiele, *et al.*, 2009) within the OMZ, but are perhaps important in generating the habitat heterogeneity which controls faunal distribution patterns (Gooday, *et al.*, 2009; 2010).

The results of the present study indicate that the change in epi-benthic megafauna and lebensspuren assemblages across the six survey stations is broadly consistent with the biofacies model of Levin *et al.* (2000), which describes a defined zonation of the benthic community based on changes of oxygen concentrations. Lebensspuren were absent at stations T1 540m and T1 800m, with the appearance of burrows observed at T2 800m and T1 1100m and the subsequent increasing densities of complex structures at 1100m and 2000m indicating a shift towards increasing bioturbation of the sediment as oxygen levels increase. This has previously been observed in oxygen minimum zones (Meadows, *et al.*, 2000; Smith, *et al.*, 2000) where bioturbation tends to increase both with changes in ambient oxygen concentrations and the abundances of megafaunal organisms. In addition, the incidence of bioturbation in the abyssal Arabian Sea, below the incidence of the OMZ, was found to be tightly correlated to benthic community composition, indicating that the megafaunal organisms act as habitat architects generating much of the habitat heterogeneity within deep-sea sediments (Turnewitsch, *et al.*, 2000).

To date, relatively few studies have investigated the benthic megafaunal assemblage, within oxygen minimum zones. Whilst these studies are quantitative and demonstrate clear changes in megafaunal abundance across an OMZ (e.g. Wishner, *et al.*, 1990; Levin, *et al.*, 1991) they provide only descriptive information about the changes in megafaunal community composition. The present study is the first study to use multivariate statistical techniques to explore the changes in community composition across an OMZ and identify which taxonomic groups drive changes in the megafaunal assemblage. Across the six survey stations megafaunal abundances were comparatively high, when compared with the abyssal Arabian Sea (0.0240 - 0.1000 ind.m⁻² (Turnewitsch, *et al.*, 2000) and exhibited a similar zonation pattern to other OMZ impacted areas (Wishner, *et al.*, 1990; Murty, *et al.*, 2009). Total megafaunal abundance peaked at 800m, exhibiting no correlation to oxygen availability. However the absence of all fauna, except fishes (Gnathostomata), at the 540m station indicates that an oxygen threshold may determine the extent of the faunal distribution within the OMZ (Levin, *et al.*, 2000; Levin, *et al.*, 2009).

Taxonomic diversity increased concomitantly with oxygen availability within the present study, with the highest diversity observed at the 1100m station. Megafaunal diversity increases with depth across the continental margin sea floor, to a mid-slope maximum (Piepenburg, *et al.*, 1996; Rex, 1997; Gage, 2001; Rex, *et al.*, 2006) and typically reaches a maximum at the boundaries of an OMZ (Levin, 2003; Gooday, *et al.*, 2009; Murty, *et al.*, 2009; Sellenes, *et al.*, 2010). In the present study, depth and oxygen concentrations were perfectly confounded but diversity was high at both the 1100m and 2000m stations, with no significant differences detected between them. Therefore, it is reasonable to infer that the increase in oxygen observed between 540m and 2000m is likely to drive the increase in assemblage diversity. This is consistent with the trend in megafaunal diversity observed at the Pakistan and Chilean margin OMZs (Murty, *et al.*, 2009; Sellenes *et al.*, 2010).

However, diversity is scale dependent (Magurran, 2004) and whilst the Shannon diversity index provides a proxy for the amount of variation within one sample of an assemblage it is a poor indicator of overall assemblage structure. The results from the multivariate cluster demonstrate that the amount of variation between replicate counts differs between stations. These data clearly show lowest similarity between replicate samples of the megafaunal assemblage at the 800m and 1100m stations, indicating that the assemblage at these depths is highly variable. It is established that changes in the geophysical environment (habitat) influence deep-sea megafaunal assemblages (Hecker, 1994; Jones, *et al.*, 2006; 2007b; 2008; Beaman and Harris, 2007; Levin and Dayton, 2009). Within an OMZ changes in the physical and geochemical environment appear to occur over relatively small spatial scales. Hence at the Indian margin, megafaunal assemblages between 800 and 1100 m are likely to be structured by chaotic ecosystem dynamics linked to localized environmental changes (McCann, *et al.*, 1998).

The results of the present study indicate that megafaunal assemblage structure is inherently complex, but changes observed across the OMZ, at the Indian margin, can be explained in terms of a number of key taxonomic groups. As previously stated, the fishes represented the only taxon present at 540m, where oxygen levels were lowest. At these low oxygen levels few organisms persist (e.g. Gooday, *et al.*, 2009) and carcasses reaching the seafloor may be preserved over long time periods (Billett, *et al.*, 2006) making the OMZ a provide a rich foraging ground for scavengers (Yeh and Drazen, 2009). On the Indian margin intact carcasses of both fish and squid were observed, on the sea floor, at the 540m station (H. Kitazato & U. Witte, *pers. obs.*) but scavenging organisms, such as Lysianassid amphipods; Macrourid and Zoarcid fishes; and shrimps of the genus *Plesiopenaeus* (Witte, 1999) were absent around these carcasses. However, fishes were relatively high in abundance

at 540m, where relatively sedentary species such as snailfishes (*Liparidae* spp.; W. R. Hunter *pers obs*) and gobies (*Gobiidae* spp.; L. Levin, *pers. comm.*) were observed. Fishes are physiologically plastic, and have been observed to be resident in OMZs in the western Pacific (Quiroga, *et al.*, 2009), thus suggesting that our observations represent a resident fish fauna in the anoxic region at 540m. Given that deep-sea fishes will feed opportunistically on both animal carrion and phytodetritus (Thurston, *et al.*, 1995; Jeffreys, *et al.*, 2010) it is likely that the observed carcasses provide a food source supporting the observed fish fauna.

In the present study, high abundances of the ophiuroids and decapod crustaceans characterised the 800m stations. These taxa are often typified as being intolerant to oxygen depletion, perishing rapidly under induced hypoxia (Riedel, *et al.*, 2008). However, large abundances of these taxa within the OMZ at the Indian continental margin are not surprising. Previous studies have identified high densities of both ophiuroids and decapods to characterise the benthos, in the boundary regions of OMZs at the Pakistan (Murty, *et al.*, 2009) and Oman margins of the Arabian Sea as well as at Volcano 7 (Wishner, *et al.*, 1990) and on the Chilean continental margin (Quiroga, *et al.*, 2009). Thus, these taxa are clearly adapted to the low oxygen concentrations within an oxygen minimum zone. In the present study, both the abundance of the ophiuroids and decapods was observed to be strongly correlated with sediment organic matter content (% TOC) and quality (C: N ratio), whilst their penetration into the OMZ may be controlled by thresholds in the ambient oxygen concentration. This is particularly striking when considered in relation to the peak in planktonic carbon content, which occurs at 800m in the Arabian Sea (Morrison, *et al.*, 1999). As such, the abundance appears to be predicted by the availability of organic matter at the sea floor and their presence is likely to have important implications for the recycling and burial of organic matter in the OMZ, as suggested by Smallwood *et al.*, (1999) and Jeffreys *et al.*, (2009b). In contrast, both sea stars (*Asteroidea*) and urchins (*Echinoidea*) were absent across much of the OMZ and where present they appeared only in low abundances. The abundance of these taxa is strongly correlated to the availability of oxygen and they characterise both 1100m stations. Thus, whilst they represent only minor taxa in terms of abundance, their presence may act as a predictor of a transitional region between the OMZ and the surrounding water mass.

To date, organic matter turnover by the epibenthic megafauna is yet to be quantified, within an oxygen minimum zone. Smallwood, *et al.*, (1999) and Jeffreys, *et al.*, (2009b) observed that where abundances of megafauna were high, the quality of sediment organic matter was reduced. Megafauna being reported to either restrict the supply of organic matter to the sediment surface or strip labile

organic compounds, such as lipids and proteins from the sediment. Oxygen minimum zones are traditionally considered to be geological sinks for organic matter (Hartnett, *et al.*, 1998). However the high densities of fauna within OMZs (Gooday, *et al.*, 2009; Murty, *et al.*, 2009; this study) may represent an important feedback by which organic matter can be recycled back into the biosphere. In the present study, the physiological carbon demand of the numerically abundant Ophiuroidea and Decapoda was estimated across the oxygen minimum zone. The rates of carbon demand observed in the present study ranged between 0.0039 and 2.2300 mmol C .m⁻² .d⁻¹ for the ophiuroids, and between 3.7300 and 54.1900 mmol C .m⁻² .d⁻¹ for the decapods. Both taxa exhibited their peak carbon demand where they were most abundant, at the 800m stations. Thus, the relative abundance of individual taxonomic groups with distinct physiological demands may influence the pathways by which organic matter is processed.

When considered in relation to organic matter turnover by the sediment community, the present study demonstrates the of the epibenthic megafauna area. During a the post-monsoon period on the Pakistan margin (September - December), sediment community respiration between 800 and 2000 m was estimated to fall within the range 1.918 - 39.319 mmol C .m⁻² .d⁻¹ (Woulds, *et al.*, 2009). Assuming this to be similar at the Indian continental margin, megafaunal carbon demand represents a significant pathway for organic matter processing which exceeds the other components of the benthic community. This is broadly consistent with the results of studies conducted in the Arctic and north Atlantic oceans, where dense aggregations of megafauna can process between 25 and 86% of the organic matter entering a benthic ecosystem (Piepenburg and Schmid 1997; Ambrose, *et al.*, 2001; Christiansen, *et al.*, 2001; Renaud, *et al.*, 2007). The present study provides only an estimate of the megafaunal role in ecosystem function, based upon previous incubation studies. This most probably underestimates the actual contribution of these megafauna to ecosystem function and it cannot account for the effects of megafaunal disturbance and feeding upon the infauna and microbial communities. However, it provides a quantitative estimate of organic matter turnover by the epibenthic megafauna which demonstrate their biogeochemical importance within an oxygen minimum zone.

5. Conclusions

In conclusion, the present study demonstrates zonation of both the epibenthic megafaunal assemblage and benthic habitat across the Indian margin OMZ. Changes in megafaunal abundance

correlate strongly with sediment organic matter quality, and diversity increased concomitantly with oxygen availability along a depth – dependent oxygen gradient. There is a structural change in the megafaunal assemblage across the OMZ, with fish the only taxa present in the OMZ core and high densities Ophiuroids and Decapods observed in the lower OMZ boundary. These results confirm that changes in both oxygen availability and sediment organic matter quality may be used as predictors of megafaunal assemblage structure (Levin 2003). The present study also indicates that changes in the megafaunal assemblage across the OMZ influence how organic matter is processed by the benthic community, supporting the hypotheses that the megafauna act as a control upon the organic matter availability in oxygen minimum zone sediments (Smallwood, *et al.*, 1999; Jeffreys, *et al.*, 2009a; b).

7. References

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Station	Site Designation	Position	Water Depth (m)			Mean Area Surveyed (m ²)
			Min	Average	Max	
T1 540m	YK08-11A	16° 58.9'N; 71° 54.3'E	530	540	600	58.75 (±5.09)
T1 800m	YK08-11C	16° 58.0'N; 71° 52.0'E	790	800	832	52.30 (±3.45)
T1 1100m	YK08-11#4	16° 57.9'N; 71° 48.5'E	1050	1100	1140	56.40 (±5.84)
T1 2000m	YK08-11#5	16° 43.5'N; 71° 17.0'E	1989	2000	2014	53.39 (±7.14)
T2 800m	YK08-11H800	17° 32.5'N; 71° 10.2'E	794	800	823	58.34 (±4.82)
T2 1100m	YK08-11H1100	17° 31.5'N; 71° 05.1'E	1005	1100	1084	80.20 (±9.27)

Table 1: Survey station summary

Phylum	Taxa Surveyed	Constituent Taxa
Porifera	Whole Phylum	Hexactinellida spp. Demospongia spp.
Cnidaria	Actinaria	Actinaria spp. <i>Actinoscyphia</i> spp.
	Pennatulacea	Pennatulacea spp.
Mollusca	Bivalvia	Pectenidea spp.
	Gastropoda	Gastropoda spp.
Arthropoda	Decapoda	<i>Plesiopenaeus</i> spp. <i>Solenocera</i> spp. <i>Encephaloides</i> spp.
	Iospoda	<i>Bathynomus</i> spp.
Echinodermata	Ophiuroidea	<i>Ophiolimna</i> spp. <i>Amphiura</i> spp.
	Asteroidea	Asteroidea spp. Brisingida spp.
	Holothuria	Holothuria spp. <i>Mesothuria</i> spp.
	Echinoidea	Echinoidea spp.
Chordata	Ascidiacea	Ascidiacea spp.
	Gnathostomata	Liparidae spp. <i>Holcomycteronus</i> spp. <i>Coryphaenoides</i> spp. Congridae spp. <i>Synaphobranchus</i> spp. <i>Etmopterus</i> spp. <i>Bathyraja</i> spp.

Table 2: Megafaunal taxa identified and counted during video surveys.

Trace Type	Description
Locomotion Trail	Linear trace on the sea-floor made by the movement of an epi-faunal or semi-infaunal animal. Most probably produced by the feeding and movements of Holothurians or Echinoids.
Holes	Burrow openings on the sediment surface. They may occur both as singular and grouped into irregular clusters.
Hole Ring	Ring of 8 – 20 burrow openings arranged in a circle. These may surround a sediment mound or a central burrow opening. Identified as an Enteropneust lebensspur (Mauviel, et al 1987).
Star-like Trace	Burrow hole surrounded by epichnial grooves, radiating outwards. Ascribed to the presence of a surface deposit feeding Echiuran worm (Ohta 1984)
Scour	Linear depression (20 – 50 cm length) within the sea floor, bordered by a rim of raised sediment. Probably formed by a fish or crustacean excavating the sediment.

Table 3: Lebensspuren groups counted during video surveys.

Station	Water Physico-Chemistry			Surficial Sediment Geochemistry (0-1cm)			
	Oxygen (μM)	Temperature ($^{\circ}\text{C}$)	Salinity	TOC (%)	TN (%)	C:N ratio	Porosity ϕ
T1 530m	0.35 (± 0.44)	11.86 (± 0.24)	35.20 (± 0.01)	4.19 (± 0.84)	0.31 (± 0.05)	14.17 (± 4.64)	72.25 (± 1.25)
T1 800m	2.09 (± 0.77)	9.83 (± 0.36)	35.08 (± 0.03)	1.52 (± 0.09)	0.19 (± 0.01)	8.18 (± 0.05)	74.96 (± 0.65)
T1 1100m	14.81 (± 1.97)	7.47 (± 0.22)	34.85 (± 0.02)	2.84	0.29	9.57	77.44
T1 2000m	107.63 (± 2.09)	2.78 (± 0.07)	34.45 (± 0.01)	1.33 (± 0.90)	0.07 (± 0.02)	19.38 (± 7.84)	68.32 (± 0.82)
T2 800m	2.63 (± 0.49)	9.81 (± 0.13)	35.08 (± 0.01)	3.54 (± 0.98)	0.42 (± 0.14)	8.41 (± 0.43)	74.93 (± 1.93)
T2 1100m	17.46 (± 4.29)	7.60 (± 0.33)	34.87 (± 0.03)	3.75 (± 2.20)	0.46 (± 0.22)	8.10 (± 0.29)	80.19 (± 1.44)

Table 4: Summary of the environmental conditions at the six survey stations. Water Physico-Chemistry data is displayed as the mean (\pm Standard Deviation) for 999 random measurements made at each station. Surficial Sediment Geochemistry is displayed as the Mean (\pm SD), based on three replicate cores.

Station	T1 540m	T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
Replicates	$n = 4$	$n = 3$				
Porifera		0.0007 (± 0.0013)			0.0066 (± 0.0063)	
Actinaria		0.0991 (± 0.0656)	0.0817 (± 0.0416)	0.0106 (± 0.0056)	0.0392 (± 0.0072)	0.0709 (± 0.0181)
Pennatulacea		0.0145 (± 0.0073)	0.0027 (± 0.0010)	0.0026 (± 0.0007)	0.0031 (± 0.0054)	0.0011 (± 0.0018)
Bivalvia				0.0036 (± 0.0037)	0.0010 (± 0.0018)	0.0049 (± 0.0190)
Gastropoda					0.0012 (± 0.0021)	
Decapoda		0.1158 (± 0.0513)	0.0363 (± 0.0096)	0.0080 (± 0.0055)	0.1480 (± 0.0107)	0.0373 (± 0.0176)
Isopoda			0.0024 (± 0.0016)			
Asteroidea			0.0058 (± 0.0071)			0.0099 (± 0.0099)
Ophiuroidea		0.4430 (± 0.4250)	0.0374 (± 0.0276)	0.0005 (± 0.0009)	0.2073 (± 0.1604)	0.0173 (± 0.0150)
Holothuria						0.0148 (± 0.0055)
Echinoidea		0.0032 (± 0.0039)	0.0046 (± 0.0046)	0.0053 (± 0.0031)		0.0151 (± 0.0043)
Crinoidea		0.0084 (± 0.0097)			0.0048 (± 0.0083)	0.0008 (± 0.0014)
Ascidiacea					0.0046 (± 0.0039)	0.0030 (± 0.0051)
Gnathostomata	0.0267 (± 0.0388)	0.0529 (± 0.0476)	0.0672 (± 0.0040)	0.0055 (± 0.0018)	0.0623 (± 0.0157)	0.0426 (± 0.0140)
Total Megafaunal Abundance	0.0267 (± 0.0039)	0.7390 (± 0.3940)	0.2380 (± 0.1489)	0.0367 (± 0.0167)	0.4780 (± 0.3130)	0.2177 (± 0.0843)
Shannon Index H' (\log_e)		1.1670 (± 0.3030)	1.4757 (± 0.0600)	1.6648 (± 0.1413)	1.2832 (± 0.1127)	1.776 (± 0.3320)

Table 5. Megafaunal abundance (ind. m⁻²) and Shannon Diversity Index (H') calculated from video survey, at six stations spanning the Arabian Sea OMZ, at the Indian Continental Margin. Data is quoted as a mean (\pm standard deviation) of n replicate surveys.

Response Variable	Statistical Test	Variance Structure	Log-Likelihood	DF	Test Statistic	p-value
Actinaria	GLS	Exponential, different strata	32.8234	5	21.2153	<0.0001
Decapoda	Kruskal-Wallis	NA	NA	5	14.0920	0.01504
Ophiuroidea	Kruskal-Wallis	NA	NA	5	15.5203	0.0084
Holothuria	Kruskal-Wallis	NA	NA	5	17.8435	0.0031
Asteroidea	Kruskal-Wallis	NA	NA	5	11.8144	0.0374
Echinoidea	Kruskal-Wallis	NA	NA	5	13.9059	0.0162
Gnathostomata	GLS	Exponential, different strata	34.2647	5	28.2422	<0.0001
Total Megafunal Abundance	GLS	Exponential, different strata	15.7430	5	8.7112	0.0008
Shannon Index $H' (log_e)$	Kruskal-Wallis	NA	NA	5	15.9398	0.0070

Table 6. Summary of the results of univariate statistical tests, comparing faunal abundance and diversity between the six survey stations.

	Depth		Oxygen		% TOC		% TN		C:N Ratio	
	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value
Actinaria	0.3131	0.1918	0.2685	0.2664	0.5268	0.0205	0.5000	0.0293	-0.5536	0.0139
Decapoda	0.1703	0.4858	0.1573	0.5202	0.6018	0.0064	0.6018	0.0064	-0.6232	0.0044
Ophiuroidea	-0.0505	0.8374	-0.0554	0.8219	0.6546	0.0024	0.5999	0.0066	-0.5561	0.0134
Asteroidea	0.5203	0.0224	0.5138	0.0244	0.2478	0.3063	0.2155	0.3756	-0.1832	0.4529
Echinoidea	0.6783	0.0014	0.6299	0.0039	-0.0470	0.8485	0.0658	0.7890	-0.2575	0.2872
Gnathostomata	-0.2844	0.2380	-0.3051	0.2040	0.4311	0.06533	0.4098	0.0814	-0.4365	0.0617
Other Taxa	0.1565	0.5222	0.1573	0.5202	0.5179	0.0231	0.5607	0.0125	-0.5982	0.0068
Total Megafunal Abundance	0.0182	0.9410	-0.0036	0.9883	0.6329	0.0036	0.6329	0.0036	-0.6756	0.0015
Shannon Index $H' (log_e)$	0.9090	<0.0001	0.9003	<0.0001	0.0661	0.7881	0.1089	0.6571	-0.1464	0.5497

Table 7. Summary of the correlations between megafaunal abundance, diversity; and the main environmental parameters across the Indian margin OMZ. All data displayed as the Spearman's Rank correlation co-efficient (ρ) and significance (p-value).

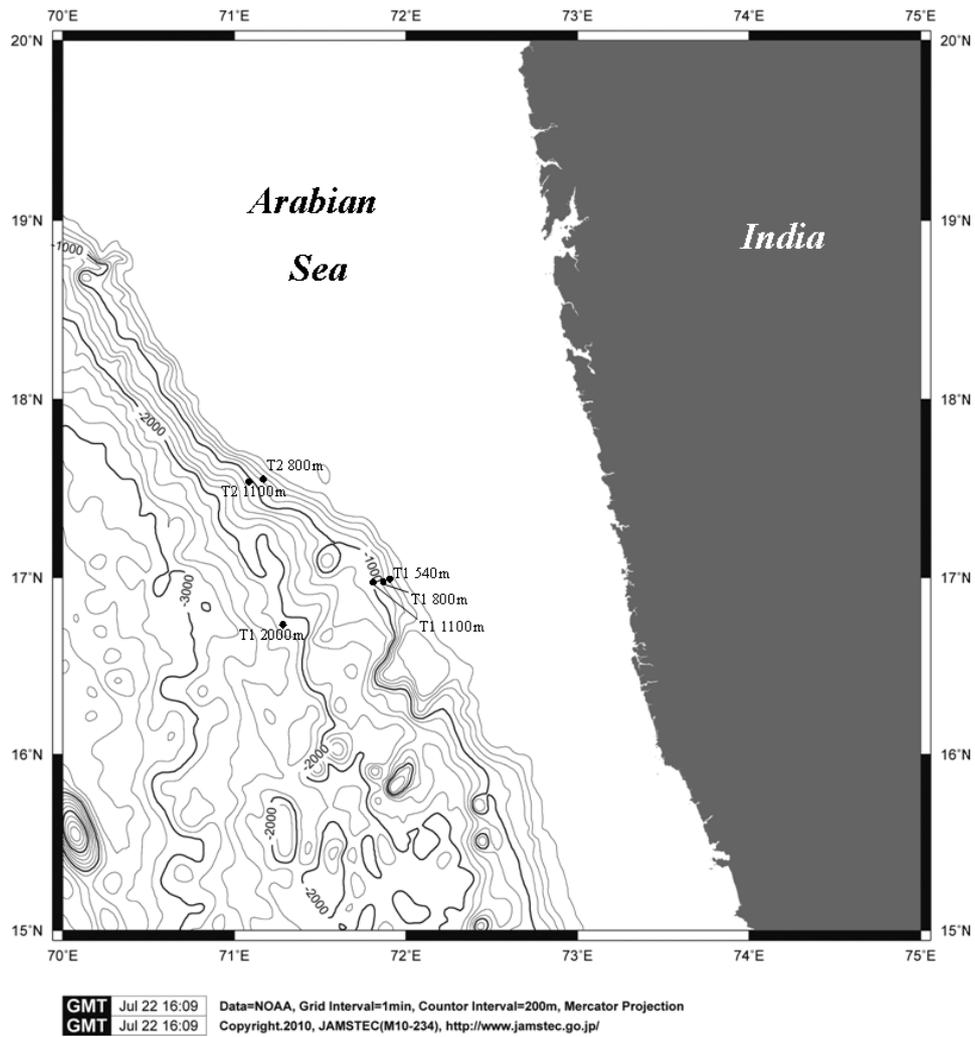


Fig. 1: Bathymetric Map of the study area. Contours represent 200 m depth intervals, with 1000 m intervals highlighted in bold.

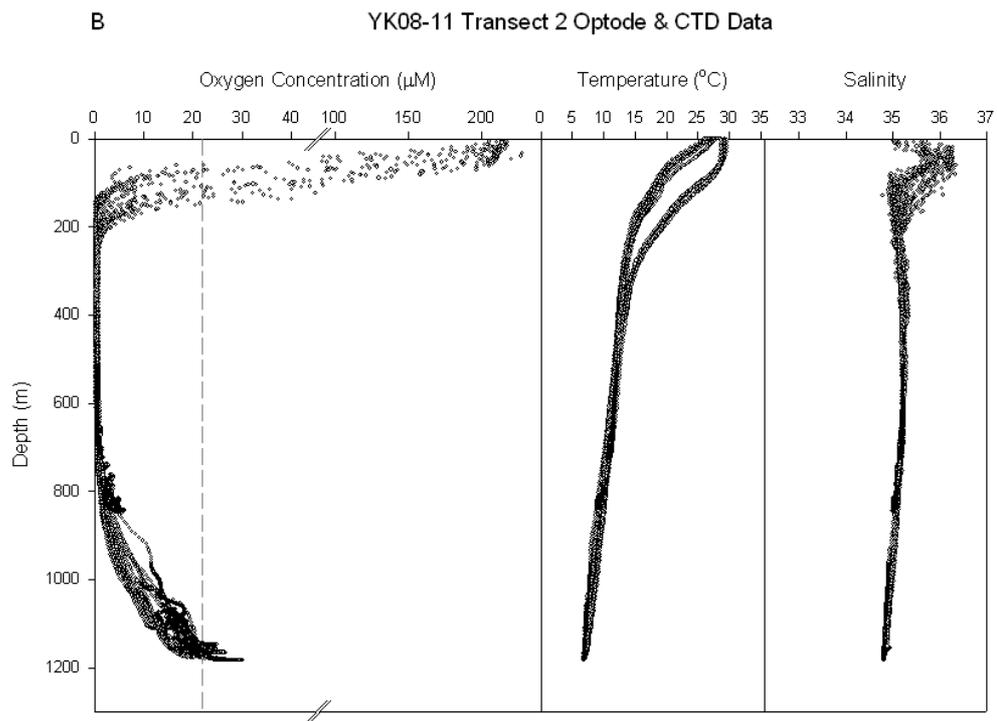
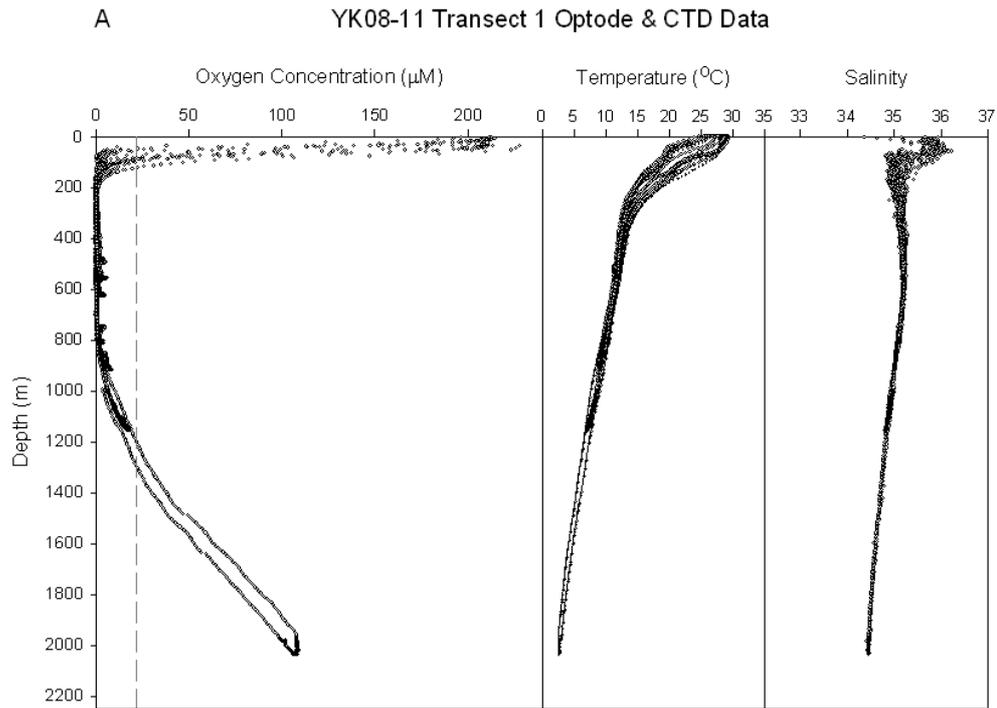


Fig. 2: Oxygen, Temperature and Salinity profiles recorded during A) Transect 1 and B) Transect 2 of cruise YK08-11. The dashed line represents an oxygen concentration of $22 \mu\text{M}$, which defines the absolute boundaries of the OMZ (Levin, 2003)



Fig. 3: Representative images of the sediment surface at the survey stations showing (A) snailfish (*Liparidae* spp.) and (B) rippled sediment at T1 540m. C) brittlestars (*Ophiolimna* spp.) at T1 800m and (D) a Brisingid sea star (*Brisingida* spp.) and flytrap anenome (*Actinoscypha* spp.) at T1 1100m. (E) a skate (*Bathyraja* spp.) and F) a scour (*Lebenspuren*) and sea star (*Asteroidea* spp.) at T1 2000m; (G) Brittlestars (*Ophiolimna* spp.) and evidence of burrows at T2 800m; and (H) fish (*Coryphaenoides* spp.) and urchin (*Echionidea* spp.) at T2 1100m.

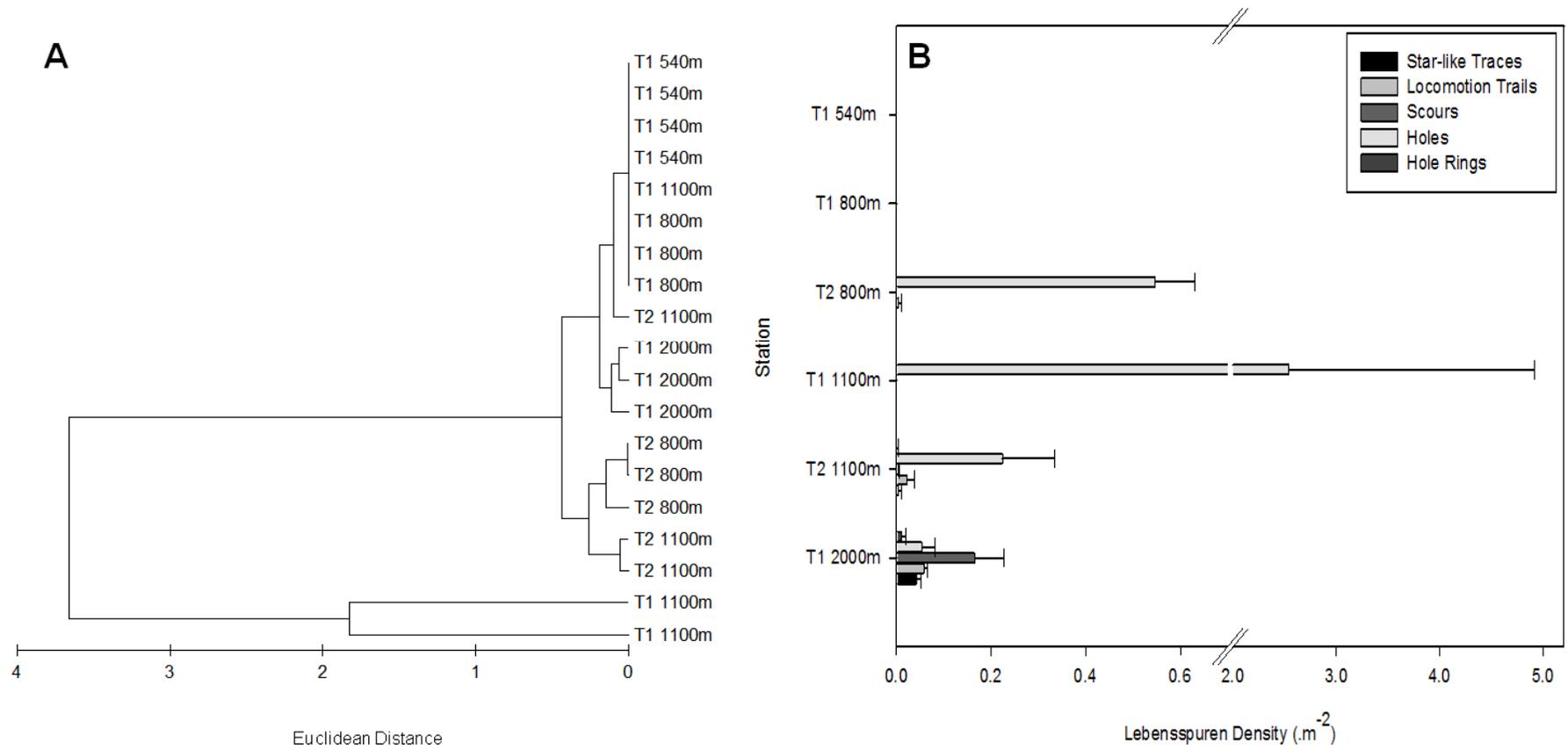


Fig. 4: A) Cluster Diagram displaying variation Lebensspuren assemblage at the six, based upon Euclidean distances between each of the six stations; and B) mean densities (\pm standard deviation) of individual trace types at the six survey stations.

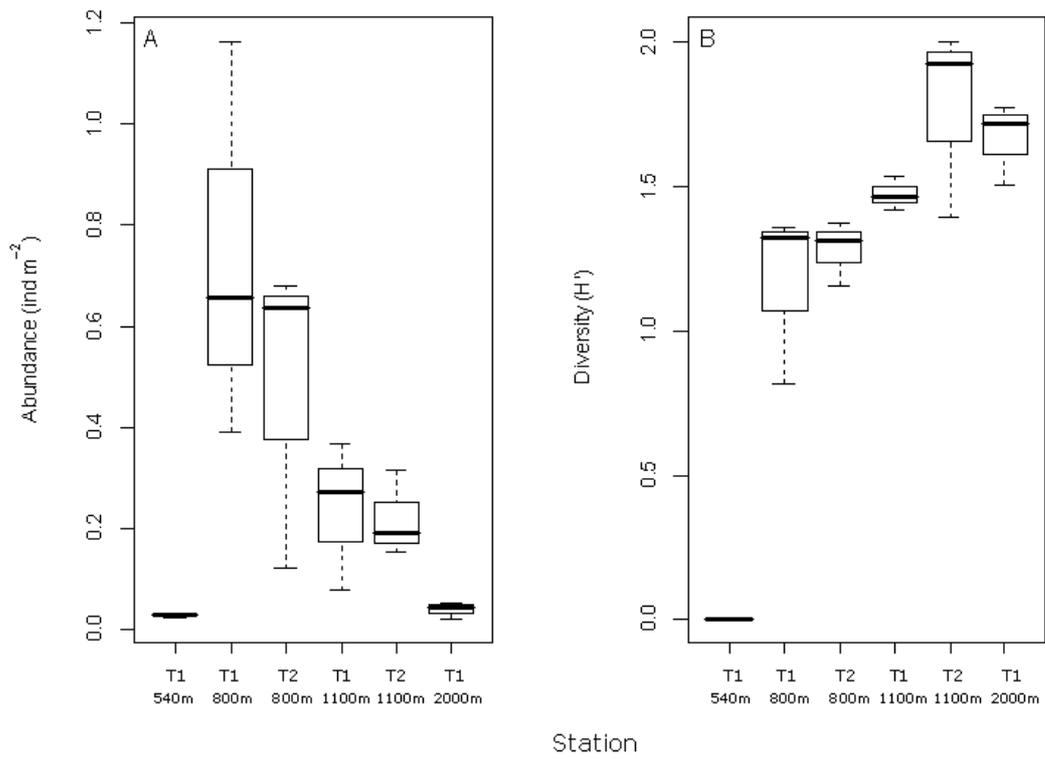


Fig. 5: (A) Total megafaunal abundance (ind.m⁻²) and (B) diversity (H' log_e) of the at the six stations across the Indian continental margin

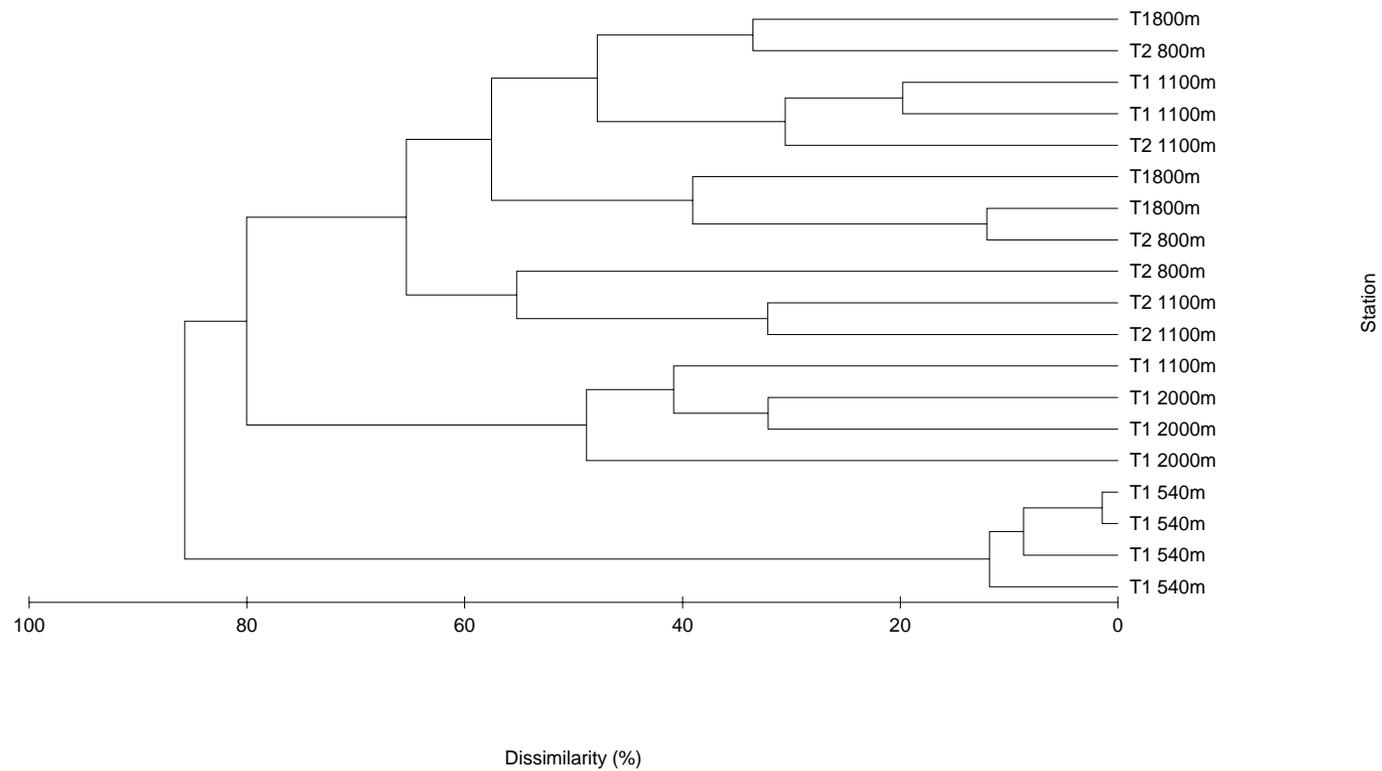


Fig. 6: Cluster analysis displaying variation in megafaunal assemblage structure, across the six survey stations. Calculated from Bray-Curtis dissimilarity index of megafaunal abundance at each station.

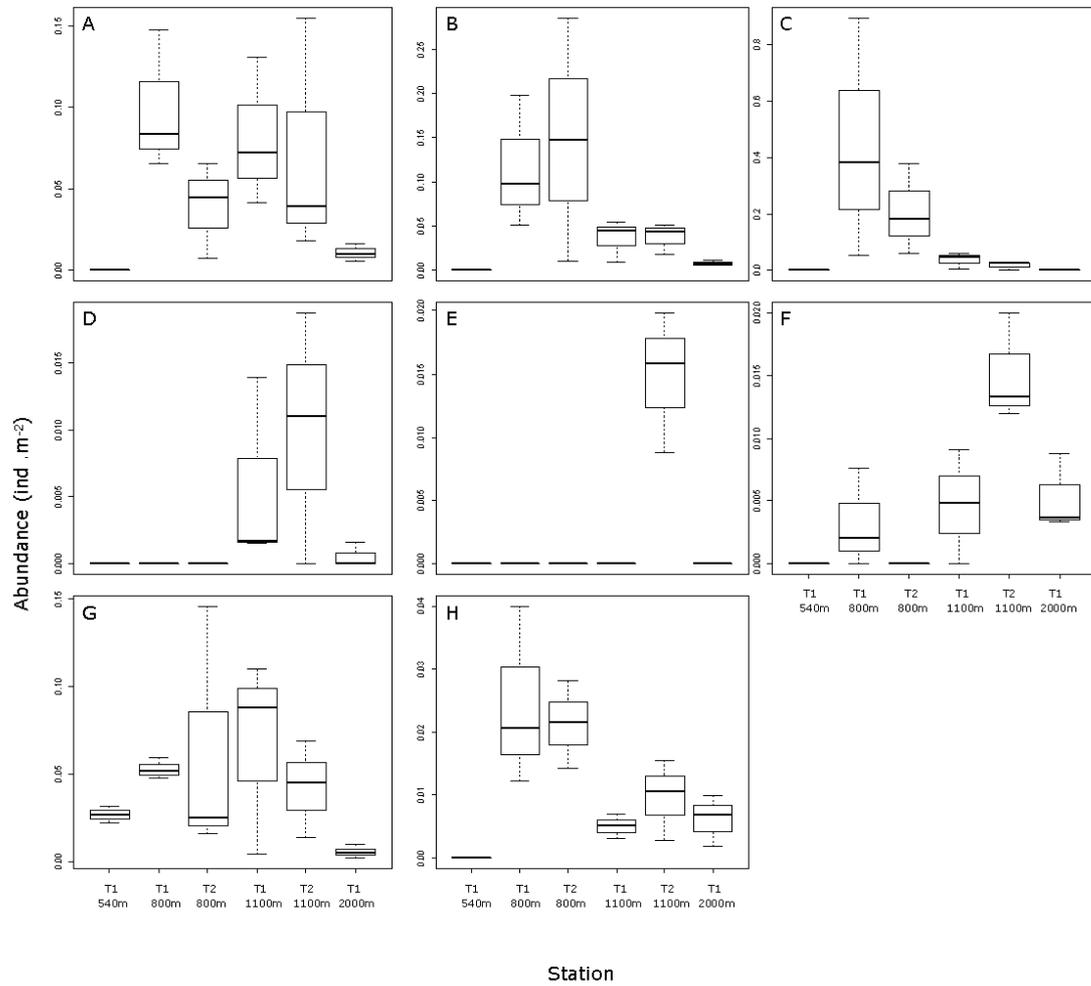


Fig. 7: Relative abundance (ind .m⁻²) of (A) Actinaria; (B) Decapoda; (C) Ophiuroidea; (D) Asteroidea; (E) Holothuria; (F) Echinoidea; (G) Gnathostomata; and (H) Other Taxa, at the six stations spanning the Indian margin OMZ.

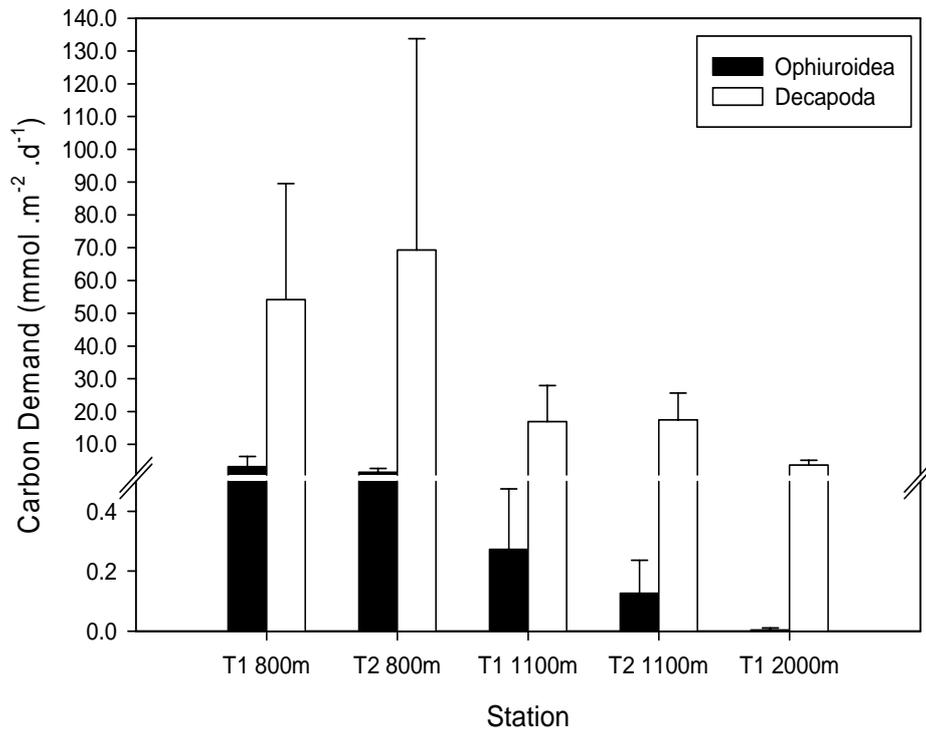


Fig. 8: Estimated organic carbon demand ($\text{mmol.m}^{-2}.\text{d}^{-1}$) of the Ophiuroidea and Decapoda at each of the five survey stations where these taxa were present. All data presented as mean and standard deviations.

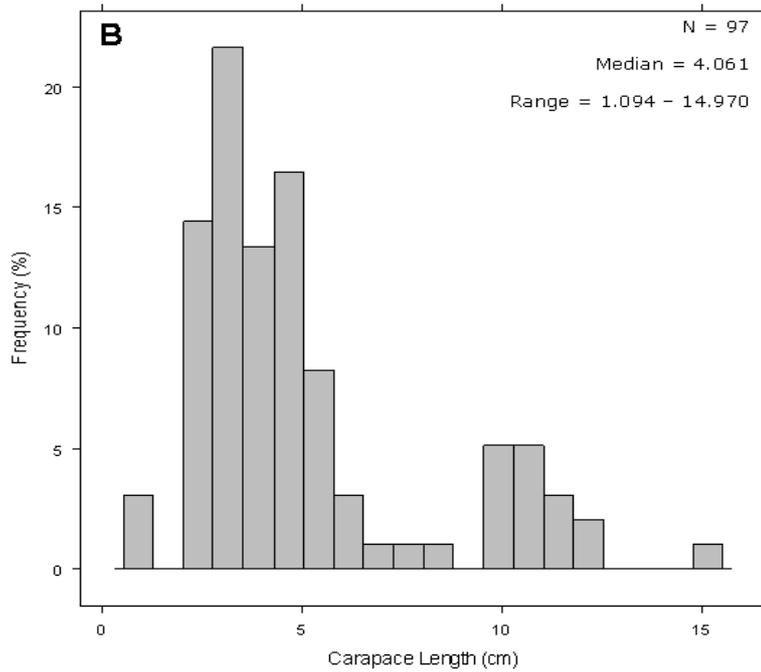
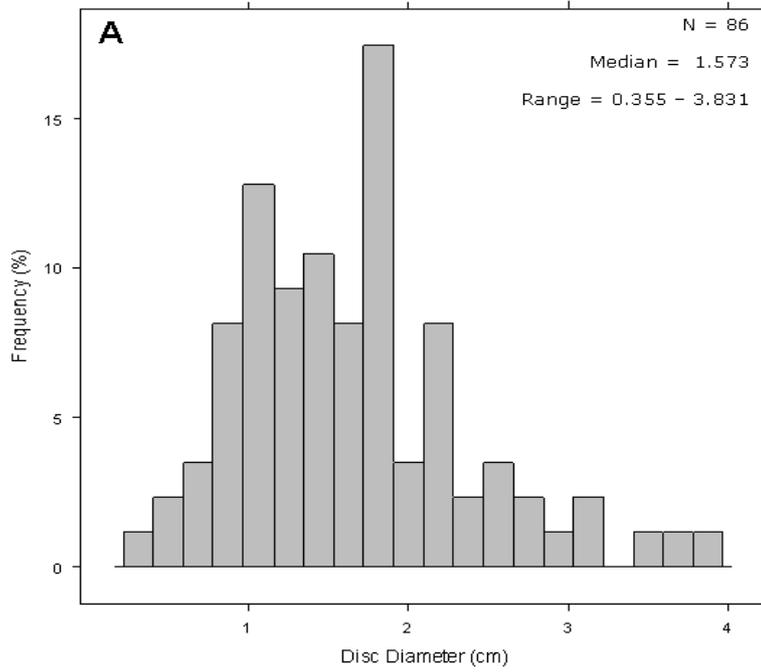
Appendices

Station	Average Similarity (%)	Contributing Taxa	Percentage Contribution (%)
T1 540m	90.97	Gnathostomata	100.00
T1 800m	48.70	Ophiuroidea	40.24
		Decapoda	21.03
		Actinaria	20.62
		Gnathostomata	14.32
T1 1100m	49.94	Actinaria	43.71
		Gnathostomata	21.03
		Decapoda	15.95
		Ophiuroidea	14.06
T1 2000m	60.71	Actinaria	30.91
		Decapoda	27.27
		Echinoidea	16.10
		Gnathostomata	12.29
		Pennatulacea	9.31
T2 800m	37.45	Ophiuroidea	52.58
		Decapoda	24.83
		Gnathostomata	11.40
		Actinaria	9.35
T2 1100m	53.97	Decapoda	21.77
		Actinaria	21.44
		Gnathostomata	19.89
		Echinoidea	10.84
		Holothuria	10.29
		Ophiuroidea	8.70

Appendix A: SIMPER Results: Average similarity in megafaunal assemblage structure between replicate surveys conducted at each station, and taxonomic groups contributing to 90% of this similarity.

	T1 540m	T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
T1 540m		Ophiuroidea (52.19%) Decapoda (24.02%) Actinaria (14.67%)	Actinaria (37.73%) Gnathostomata (24.47%) Decapoda (14.67%) Ophiuroidea (14.56%)	Gnathostomata (43.20%) Actinaria (19.20%) Decapoda (14.82%) Echinoidea (10.17%) Bivalvia (6.16%)	Ophiuroidea (49.18%) Decapoda (27.58%) Actinaria (8.34%) Gnathostomata (8.13%)	Actinaria (31.20%) Decapoda (18.50%) Gnathostomata (11.50%) Ophiuroidea (10.98%) Holothuria (8.64%) Echinoidea (8.48%) Asteroidea (6.12%)
T1 800m			Ophiuroidea (57.57%) Decapoda (19.82%) Gnathostomata (8.99%) Actinaria (7.53%)	Ophiuroidea (51.90%) Decapoda (22.40%) Actinaria (12.77%) Gnathostomata (8.27%)	Ophiuroidea (51.63%) Decapoda (22.17%) Actinaria (10.75%) Gnathostomata (9.05%)	Ophiuroidea (55.86%) Decapoda (17.65%) Actinaria (10.86%) Gnathostomata (3.91%) Holothuria (2.71%)
T1 1100m				Actinaria (36.6%) Gnathostomata (25.73%) Ophiuroidea (16.72%) Decapoda (12.24%)	Ophiuroidea (35.25%) Decapoda (24.90%) Gnathostomata (16.07%) Actinaria (14.40%)	Actinaria (27.16%) Gnathostomata (24.32%) Ophiuroidea (13.61%) Decapoda (10.51%) Holothuria (8.19%) Echinoidea (5.21%) Asteroidea (4.93%)
T1 2000m					Ophiuroidea (46.73%) Decapoda (23.86%) Gnathostomata (13.15%) Actinaria (6.11%) Crinoidea (3.60%)	Actinaria (27.81%) Gnathostomata (18.73%) Decapoda (15.45%) Ophiuroidea (11.64%) Holothuria (9.30%) Asteroidea (6.43%) Echinoidea (6.07%)
T2 800m						Ophiuroidea (35.62%) Decapoda (23.47%) Actinaria (13.42%) Gnathostomata (10.54%) Holothuria (4.03%) Echinoidea (4.02%)

Appendix B: SIMPER results II: Similarity matrix, detailing the taxonomic groups responsible for 90% of the cumulative difference in megafaunal assemblage structure between survey stations



Appendix C: Size frequency distributions of the A) Ophiuroidea and B) Decapoda, calculated from individuals observed in video frame-grabs.

Supplementary Data.

	df	SS	MS	pseudo-F	R ²	p-value
Station	5.0000	15.0935	3.0187	3.4512	0.5703	0.0319
Resid.	13.0000	11.3707	0.8747		0.4297	
Total	18.0000	26.4642			1.0000	

Suppl. 1: perMANOVA model output for Lebenspurren density against station, for 1000 permutations of a similarity matrix derived from Euclidean distance between stations.

A)

ANOVA model fitted by Generalized Least Squares,
maximizing the Restricted Log-Likelihood.

Model: Actinaria ~ Station

Denom. DF: 13

	DF	F-value	p-value
Intercept	1	24.1426	0.0003
Station	5	21.2152	<0.0001

AIC	BIC	logLik
-39.6467	-32.3023	32.8233

Variance Structure: Exponential function of Vertebrate
Abundance, at each of the six stations.

Formula: ~ Actinaria | Station

Parameter estimates:

T1 540m	T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
0.0000	21.7138	27.7478	57.4848	51.0736	29.0181

Multiple Comparisons for station T1 540m

	Value	SE	t-value	p-value
Intercept	0.0000	0.0014	0.0000	1.0000
T1 800m	0.0727	0.0098	7.3987	0.0015
T1 1100m	0.0468	0.0084	5.5668	0.0015
T1 2000m	0.0086	0.0032	2.6936	0.2760
T2 800m	0.0081	0.0043	1.8811	1.0000
T2 1100m	0.0229	0.0045	5.1357	0.0030

Multiple Comparisons for station T1 800m

	Value	SE	t-value	p-value
T1 1100m	-0.0259	0.0128	-2.0284	0.9525
T1 2000m	-0.0641	0.0101	-6.3283	0.0015
T2 800m	-0.0647	0.0105	-6.1340	0.0015
T2 1100m	-0.0498	0.0106	-4.6946	0.0060

Multiple Comparisons for station T1 1100m

	Value	SE	t-value	p-value
T1 2000m	-0.0382	0.0088	-4.3612	0.0120
T2 800m	-0.0387	0.0092	-4.1967	0.1500
T2 1100m	-0.0239	0.0093	-2.5659	0.3525

Multiple Comparisons for station T1 2000m

	Value	SE	t-value	p-value
T2 800m	-0.0005	0.0049	-0.1007	1.0000
T2 1100m	0.0144	0.0051	2.8109	0.2205

Multiple Comparisons for station T2 800m

	Value	SE	t-value	p-value
T2 1100m	0.0149	0.0059	2.5323	0.3750

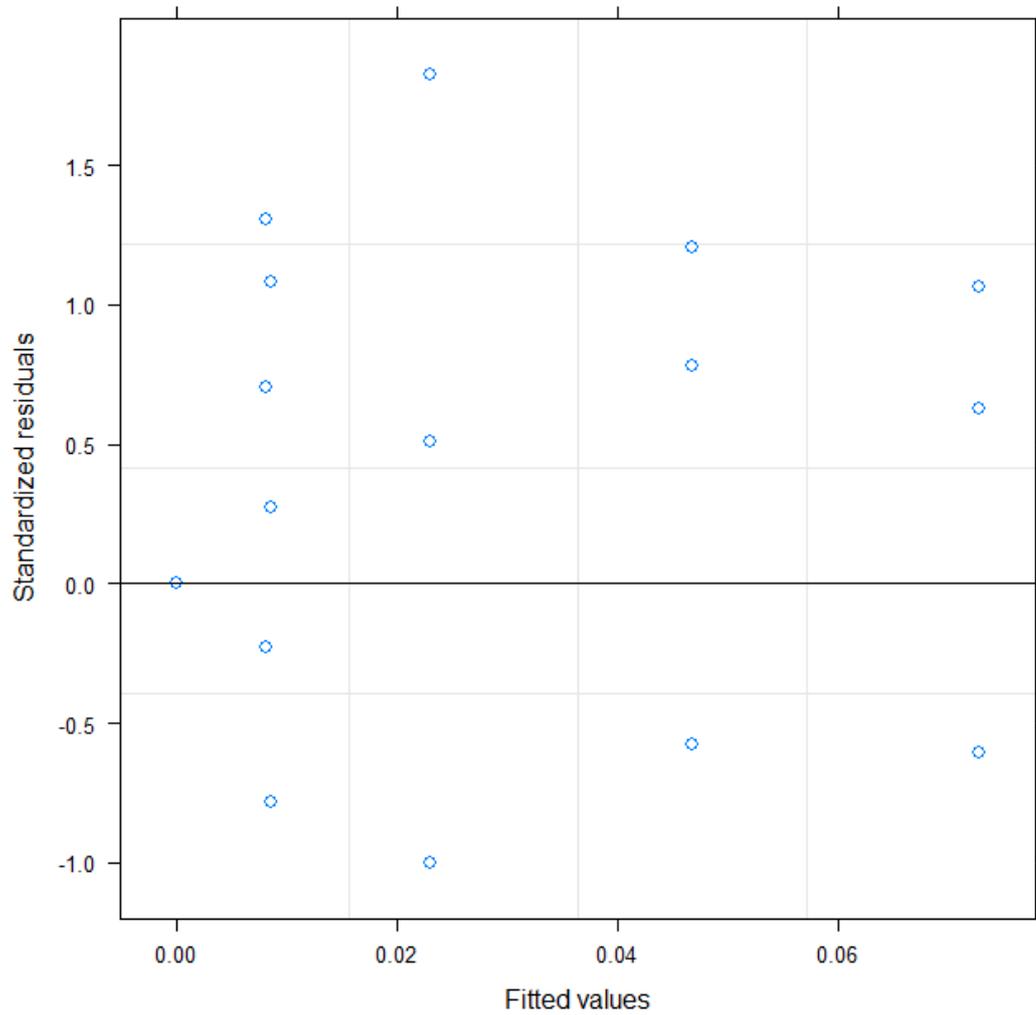
Standardized residuals:

Min	Q1	Med	Q3	Max
-1.0018	-0.1133	0.2729	0.9213	1.8269

Residual standard error: 0.0028

Degrees of freedom: 19 total; 13 residual

B)



Suppl 2: A) Model summary and B) model fit, for the Generalized Least Squares ANOVA comparing abundance of Actinaria across the six survey stations. All t-test values are Bonferroni corrected for 15 comparisons.

A)

ANOVA model fitted by Generalized Least Squares,
maximizing the Restricted Log-Likelihood.

Model: Gnathostomata ~ Station

Denom. DF: 13

	DF	F-value	p-value
Intercept	1	297.3436	<0.0001
Station	5	29.5298	<0.0001

AIC	BIC	logLik
-44.8600	-37.5157	35.4300

Variance Structure: Exponential function of Vertebrate
Abundance, at each of the six stations.

Formula: ~ Gnathostomata | Station

Parameter estimates:

T1 540m	T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
-0.0303	8.0381	32.4074	10.1753	23.7781	40.2264

Multiple Comparisons for station T1 540m

	Value	SE	t-value	p-value
Intercept	0.0268	0.0019	13.6068	0.0015
T1 800m	0.0257	0.0039	6.4433	0.0015
T1 1100m	-0.0223	0.0049	-4.5772	0.0075
T1 2000m	-0.0215	0.0031	-6.9194	0.0015
T2 800m	-0.0073	0.0048	-1.4986	1.0000
T2 1100m	-0.0099	0.0069	-1.4324	1.0000

Multiple Comparisons for station T1 800m

	Value	SE	t-value	p-value
T1 1100m	-0.0481	0.0057	-8.4947	0.0015
T1 2000m	-0.0472	0.0042	-11.1783	0.0015
T2 800m	-0.0330	0.0057	-5.8424	0.0015
T2 1100m	-0.0356	0.0075	-4.7699	0.0060

Multiple Comparisons for station T1 1100m

	Value	SE	t-value	p-value
T1 2000m	0.0009	0.0051	0.1678	1.0000
T2 800m	0.0150	0.0063	2.3815	1.0000
T2 1100m	0.0125	0.0079	1.5636	1.0000

Multiple Comparisons for station T1 2000m

	Value	SE	t-value	p-value
T2 800m	0.0142	0.0051	2.7991	0.2265
T2 1100m	0.0116	0.0070	1.6528	1.0000

Multiple Comparisons for station T2 800m

	Value	SE	t-value	p-value
T2 1100m	-0.0026	0.0079	-0.3219	1.0000

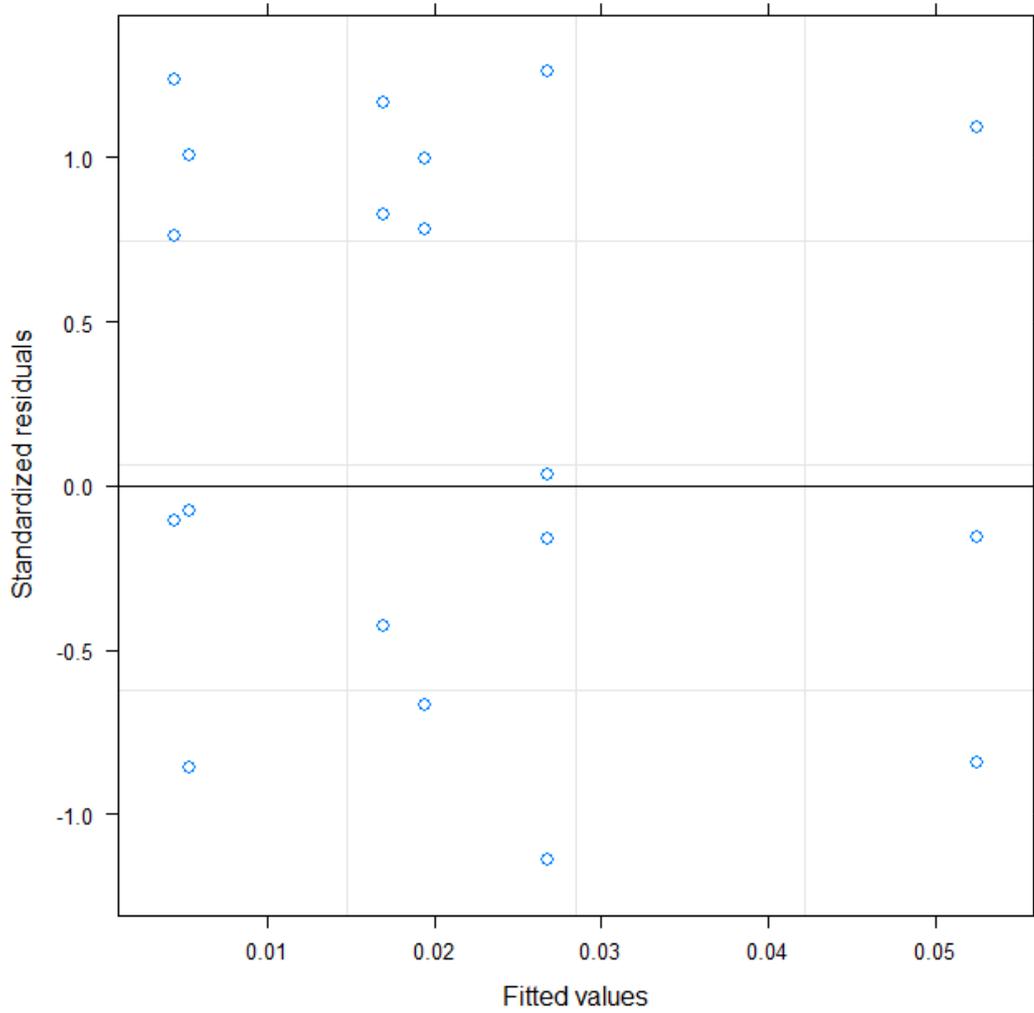
Standardized residuals:

Min	Q1	Med	Q3	Max
-1.1393	-0.2923	0.0344	1.0020	1.2636

Residual standard error: 0.0039

Degrees of freedom: 19 total; 13 residual

B)



Suppl 3: A) Model summary and B) model fit, for the Generalized Least Squares ANOVA comparing abundance of Gnathostomata (Fishes) across the six survey stations. All t-test values are Bonferroni corrected for 15 comparisons.

A)

ANOVA model fitted by Generalized Least Squares,
maximizing the Restricted Log-Likelihood.

Model: Total Abundance ~ Station

Denom. DF: 13

	DF	F-value	p-value
Intercept	1	311.6152	<0.0001
Station	5	8.7111	0.0008

AIC	BIC	logLik
-5.4860	1.8583	15.7430

Variance Structure: Exponential function of the total
megafaunal abundance, at each of the six stations.

Formula: Total Abundance | Station

Parameter estimates:

T1 540m	T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
-93.4813	2.2544	4.3756	-40.3045	3.5369	2.2326

Multiple Comparisons for Station T1 540m

	Value	SE	t-value	p-value
Intercept	0.0289	0.0019	15.2940	0.0015
T1 800m	0.4406	0.1069	4.1202	0.0180
T1 1100m	0.0924	0.0633	1.4606	1.0000
T1 2000m	0.0176	0.0056	3.1329	0.1185
T2 800m	0.1121	0.0759	1.4773	1.0000
T2 1100m	0.1699	0.0469	3.6222	0.0465

Multiple Comparisons for Station T1 800m

	Value	SE	t-value	p-value
T1 1100m	-0.3482	0.1242	-2.8026	0.2250
T1 2000m	-0.4229	0.1071	-3.9509	0.0255
T2 800m	-0.3285	0.1311	-2.5063	0.3945
T2 1100m	-0.2707	0.1167	-2.3191	0.5595

Multiple Comparisons for Station T1 1100m

	Value	SE	t-value	p-value
T1 2000m	-0.0748	0.0635	-1.1781	1.0000
T2 800m	0.0196	0.0988	0.1989	1.0000
T2 1100m	0.0774	0.0787	0.9838	1.0000

Multiple Comparisons for Station T1 2000m

	Value	SE	t-value	p-value
T2 800m	0.09442	0.07602	1.2419	1.0000
T2 1100m	0.15222	0.04716	3.2279	0.0990

Multiple Comparisons for Station T2 800m

	Value	SE	t-value	p-value
T2 1100m	0.05781	0.0891	0.6485	1.0000

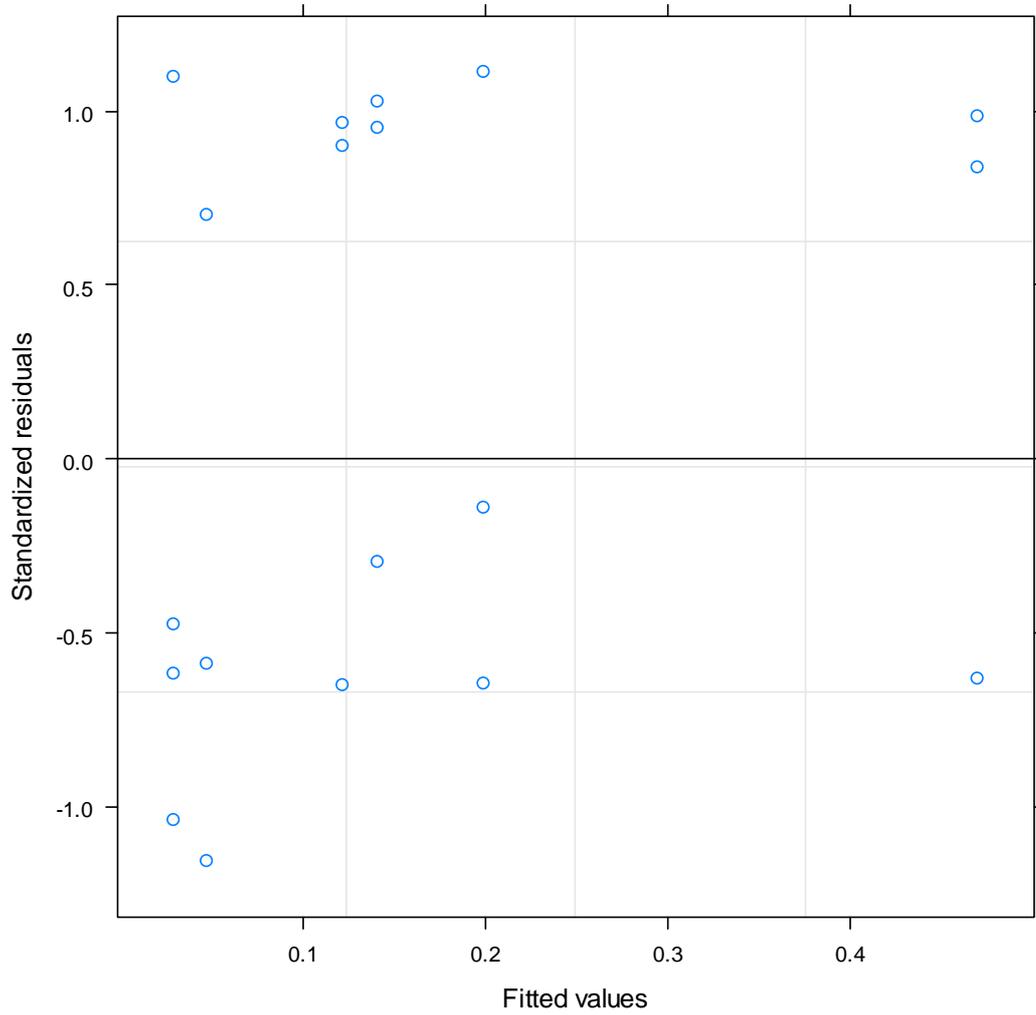
Standardized residuals:

Min	Q1	Med	Q3	Max
-1.1574	-0.6235	-0.1426	0.9591	1.1121

Residual standard error: 0.0510

Degrees of freedom: 19 total; 13 residual

B)



Suppl 4: A) Model summary and B) model fit, for the Generalized Least Squares ANOVA comparing total megafaunal abundance across the six survey stations. All t-test values are Bonferroni corrected for 15 comparisons.

A)

ANOVA model fitted by Generalized Least Squares,
maximizing the Restricted Log-Likelihood.

Model: C_Demand ~ Station + Taxa + Station:Taxa

Denom. DF: 20

	DF	F-value	p-value
Intercept	1	1.0274	0.3229
Station	4	5.1292	0.0052
Taxa	1	45.8628	<0.0001
Station:Taxa	4	4.1485	0.0132

AIC	BIC	logLik
126.9562	142.8879	-47.47809

Variance Structure: Variance allowed to differ both across stations and between taxonomic groups

Formula: $\sim 1 \mid \text{Station}$

Parameter estimates:

T1 800m	T1 1100m	T1 2000m	T2 800m	T2 1100m
1.0000	0.0869	0.0081	0.5062	0.0560

Formula: $\sim 1 \mid \text{Taxa}$

Parameter estimates:

Decapod	Ophiuroid
1.0000	0.0169

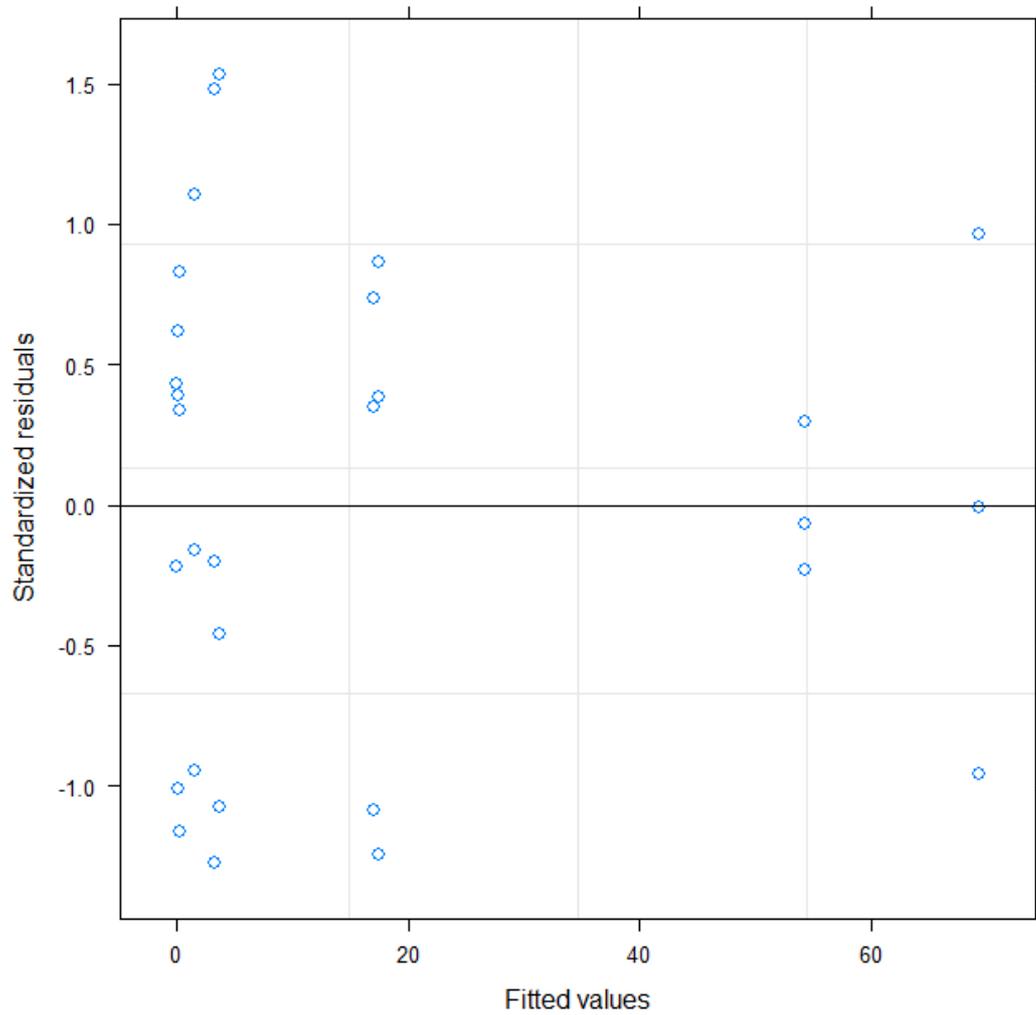
Standardized residuals:

Min	Q1	Med	Q3	Max
-1.2757	-0.8249	-0.0361	0.5740	1.5345

Residual standard error: 132.3970

Degrees of freedom: 30 total; 20 residual

B)



Suppl 5: A) Model summary and B) model fit, for the two-way Generalized Least Squares ANOVA comparing physiological carbon demand by the Ophiuroidea and Decapoda across the six survey stations. All t-test values are Bonferroni corrected for 15 comparisons.