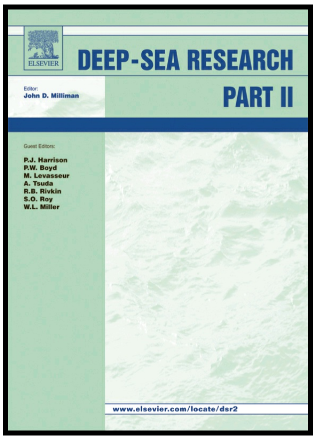

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Composition of abyssal macrofauna along the Vema Fracture Zone and the hadal Puerto Rico Trench, northern tropical Atlantic

Brandt, A.[1,2*], Frutos, I.[1], Bober, S.[1], Brix, S.[3], Brenke, N.[3], Guggolz, T.[1], Heitland, N.[1], Malyutina, M.[4], Minzlaff, U.[1], Riehl, T.[1], Schwabe, E.[5], Zinkann, A.-C.[6], Linse, K.[7]

[1]Zoological Museum Hamburg, Center of Natural History, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany.

[2]Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt, Germany

[3]German Centre for Marine Biodiversity Research, c/o University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany

[4]A.V. Zhirmunsky Institute of Marine Biology, FEB RAS, Palchevskogo 17, 690041, Far East Federal University, Oktiabrskaya Str, 29, 690600,Vladivostok, Russia

[5]Bavarian State Collection of Zoology, Münchhausenstrasse 21, 81247 München, Germany

[6]Universtiy of Alaska Fairbanks, College of Fisheries and Ocean Sciences, 905 N. Koyukuk Drive, 245 O'Neill Bldg., 99775 Fairbanks, Alaska, USA

[7]British Antarctic Survey, High Cross, Mandingley Road, Cambridge CBE 0ET, United Kingdom

[*]Corresponding author E-mail: Abrandt@uni-hamburg.de

Abstract

We analyzed composition and variations in benthic macrofaunal communities along a transect of the entire length of the Vema-Fracture Zone on board of RV *Sonne* (SO-237) between December 2014 and January 2015 in order to test whether the Mid-Atlantic Ridge serves as a barrier limiting benthic taxon distribution in the abyssal basins on both sides of the ridge or whether the fracture zone permits the migration of species between the western and eastern abyssal Atlantic basins. The Puerto Rico Trench, much deeper than the surrounding abyssal West Atlantic, was sampled to determine whether the biodiversity of its hadal macrofauna differs from that of the abyssal Atlantic.

The composition of the macrofauna from the epibenthic sledge catches yielded a total of 21,332 invertebrates. Crustacea occurred most frequently (59%) with 12,538 individuals followed by Annelida (mostly Polychaeta) (26%) with 5,491 individuals, Mollusca (7%) with 1,458 individuals, Echinodermata (4%) with 778 individuals, Nematoda (2%) with 502 individuals and Chaetognatha (1%) with 152 and Porifera (1%) with 131 individuals. All other taxa occurred with overall less than ten individuals (Hemichordata, Phoronida, Priapulida, Brachiopoda, invertebrate Chordata, Echiurida, Foraminifera (here refereed to macrofaunal Komokiacea only), Chelicerata, Platyhelminthes). Within the Crustacea, Peracarida (62.6%) with 7,848 individuals and Copepoda (36.1%) with 44,526 individuals were the most abundant taxa. Along the abyssal Vema-Fracture Zone macrofaunal abundances (ind./1,000 m^2) were generally higher on the eastern side, while the highest normalized abundance value was reported in the Puerto Rico Trench at abyssal station 14-1 2,313 individuals/1,000 m^2. The lowest abundance was reported at station 11-4 with 120 ind./1,000 m^2 located at the western side of the Vema-Fracture Zone. The number of major macrofaunal taxa (phylum, class) ranged between five (stations 12-5, 13-4 and 13-5 at hadal depths in the Puerto Rico Trench) and 14 (station 9-8) in the western abyssal basin of the Vema-Fracture Zone. Differences are seen in the distribution of Porifera at macrofaunal level between eastern and western sides of the Vema-Fracture Zone. Macrofaunal composition of the study area is compared with data from other expeditions in the Atlantic and the northwest Pacific Ocean.

Keywords: Atlantic Ocean, Mid-Atlantic Ridge, deep sea, taxon composition, benthic communities, invertebrates, C-EBS

1. Introduction

The abyssal seafloor is the largest environment on Earth; however, it is much less explored than our continental shelves and slopes. Knowledge about life on the deep seafloor (McClain and Schlachter, 2015) where many species still remain undiscovered (Ramirez-Llodra et al., 2010) is still scarce in many areas. Furthermore, it is unknown how the hydrosphere, biosphere and lithosphere interact over this vast area. The Atlantic Ocean seabed is characterized by transform faults and fracture zones. The volcanic and tectonic processes which create and modify the crust are the driving forces of today's bathymetry. One of the factors influencing the benthic and suprabenthic species and communities are tectonic processes, but it is unknown to which extent and how it determines the distribution of benthic species.

Deep-sea macrofaunal communities have been investigated in several areas of the world by means of an epibenthic sledge focusing especially on the composition of peracarid crustaceans (Brandt, 1992, 1993, 1995, 1997; Brandt and Barthel, 1995; Brenke, 2005, Brandt et al. 2005, 2007, 2012, 2013; Brökeland et al., 2007; Frutos et al., 2017). However, in the past, no studies have been conducted in the abyssal Atlantic Ocean focusing on the sampling of a latitudinal transect across basins separated by the Mid Atlantic Ridge during a single expedition using an epibenthic sledge. During the SO237 expedition with RV *Sonne* we surveyed the entire length of one of the major offsets of the Mid-Atlantic Ridge (MAR), the Vema Fracture Zone (VFZ) (Devey et al 2015, Devey et al., present volume) as well as variations in benthic communities along this transect.

One of our major objectives was to study the abundance, taxon richness and composition of the benthic macrofauna along an abyssal east-west transect across the Mid-Atlantic Ridge as well as in the Puerto Rico Trench (PRT).

We hypothesize that the MAR usually acts as a physical barrier and can isolate the benthic faunas in the eastern and western abyssal basins from each other. However, we also hypothesize that currents, e.g. the Antarctic Bottom Water, following the VFZ crossing the MAR at abyssal depth could serve as a passage for the migration of benthic organisms from one side of the MAR to the other. As the PRT is much deeper than the surrounding abyssal West Atlantic, we expect that the hadal fauna is isolated in this environment from the abyssal benthic fauna sampled in the PRT and VFZ.

For this reason we determine whether the composition of its hadal macrobenthic fauna differs from that of the abyssal Atlantic, compare the new macrofaunal data from the VFZ with epibenthic sledge catch compositions from other Atlantic areas and compare our results with the general taxon composition from Atlantic, Pacific and Southern Ocean areas sampled with similar epibenthic sledges (e.g. Brandt et al., 2005; Brökeland et al., 2007; Brandt et al., 2007, 2012; Brenke, 2005).

2. Material and Methods

The maiden expedition of the German RV *Sonne* (SO-237), Vema-TRANSIT (Bathymetry of the Vema-Fracture Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study), sailed from 15.12.2014 to 26.01.2015 across the Atlantic following along the length of the VFZ crossing the Mid-Atlantic Ridge to the Puerto Rico Trench.

2.1. Study area

Sampling was performed along the VFZ and the Vema Transform Fault (VTF) in the tropical North Atlantic (Devey et al., 2015). Five sites were sampled respectively in the eastern and western VFZ and one station within the VTF (Table 1 and Figure 1). The VFZ and VTF are roughly located at latitude 11° N (exact station locations are provided in Table 1). It is part of a group of transform faults which offsets the Mid-Atlantic Ridge by 320 km (Louden et al., 1986; Cannat et al., 1991). It is composed of a flat transform valley bounded by steep walls with some peaks reaching as high as 500 m below surface (Morozov et al., 2010). Both, the VFZ and VTF are strongly affected by the advection of the Antarctic Bottom Water, which flows into the VTF from the western side. This Antarctic water mass flows below 4,300 m and is characterized by low temperature, low salinity, and high nutrient content if compared to the overlaying North Atlantic Deep Water (Morozov et al., 2010, 2015). The physical environment of the VFZ including the bathymetry is described in detail by

Devey et al. (present volume). The general hydrography of the northern North Atlantic (Schäfer et al., 2001) and South Atlantic (Wefer et al., 1996) is published in two books.

2.2. Deployment of C-EBS

A camera-epibenthic sledge (C-EBS) designed for sampling small epi- and suprabenthic macrofauna (from half a millimetre to centimetres of size) at any depth and on any substrate was used (Brandt et al., 2013). The C-EBS was equipped with supra- and epibenthic samplers possessing two plankton nets (500 µm) with cod ends (300 µm) placed in temperature-isolated thermo-boxes for work in tropical waters, but keeping the animals in cold bottom water for later studies including molecular genetics. An opening-closing mechanism, active at bottom contact, prevented captures of pelagic fauna. The haul distances were calculated using the time and the speed (ships speed with 1 knot, and winch speed with -0.5 m/sec. (equals one knot)) (as outlined in Devey, 2015) until the C-EBS left the ground, which was indicated by the tension meter. At station 9-2 on the western side of the VFZ the C-EBS got stuck and remained on the ground for almost three hours until it was possible to retrieve it back on the vessel and trawling time could not be determined. In this case, the haul length was calculated by means of a TSK flowmeter placed in the upper net, even though this could be affected by bottom currents. Trawled distances were used to calculate the area sampled by the sledge (1 m width, see Brenke, 2005). To allow the comparison between stations, data were standardized to 1,000 m^2.

Additionally, the C-EBS carries an autonomous digital underwater video camcorder and a still camera, both equipped with the required energy and control units as well as a Seaguard RCM DW for measuring data on temperature (°C), pressure (hPa), conductivity (mS/cm), current velocity (m/s) and oxygen (µM) concentration when the sledge is on ground. As these electronic devices can only be deployed until 6,000 m depth, they were not deployed at hadal depths in the Puerto Rico Trench.

Every haul is considered to be a station, 2-6 and 2-7 are two stations at the same site.

2.3. Sample treatment and comparability

On deck the samples were immediately transferred into pre-cooled (-20°C) 96% ethanol and kept for at least 24 h in a -20°C freezer for subsequent DNA studies. In the laboratories of the ship and later in the home institutes, sorting of the macrofauna was done on ice in order to avoid DNA decomposition (Riehl et al., 2014). For macrofaunal analysis, the complete supra- and epinet samples were sorted and data were pooled for every station. The material was sorted and identified in major taxa using stereomicroscopes.

For comparison between stations, abundance data were expressed as individuals per 1,000 m² trawled distances.

2.4. Statistics

Datasets comparable to the one presented here were available from previous expeditions that used similar sampling protocols, e.g. to the South Polar Front, the Scotia Arc area and Subantarctic, the Cape, Angola, Guinea, Argentinian and Brazilian basins and in the NW Pacific the Sea of Japan and the Kuril-Kamchatka abyssal plain either as published data (Brandt et al., 2013, 2015) or from the Forschunginstitut Senckenberg, Deutsches Zentrum für Marine Biodiverstätsforschung and British Antarctic Survey expedition databases (unpublished data). PRIMER v6 (Clarke and Gorley, 2006) was used to compare the macrofaunal assemblages of each of the Vema-TRANSIT stations, between Vema-TRANSIT and previous expeditions, as well as abyssal assemblages separately. The Bray-Curtis similarity coefficient is applied to standardized abundance data of all macrofaunal taxa present in the EBS samplers obtaining a similarity matrix (Clarke and Gorley, 2006). Hierarchical clustering with group-averaged linking and non-metric multidimensional scaling (nMDS) was then performed using these matrixes. One-way ANOSIM tests were performed (Vema-Transit, global multi-expedition and global abyssal only multi-expedition) in order to investigate the differences between groups of stations. Depth zones are defined as Southern Ocean shelf (200 m – <1000 m depth), bathyal (200 m – <3,000 m depth), abyssal (3,000 m – <6,000 m depth), and hadal (>6,000 m depth). Areas are defined as Puerto Rico trench (PRT), south Atlantic (S_Atl), southeast Atlantic (SE_Atl), southwest Atlantic (SW_Atl), Southern Ocean (SO), northwest Pacific (NW_Pac), Vema Fracture Zone (VFZ).

Regions are defined as Aghulas Basin, Angola Basin, Argentine Basin, Brazil Basin, Cape Basin.

2.5. Terminology

We use the term “common” if we talk about a number of individuals per station of ~100, with the term “rare” we refer to singletons, doubletons or <10 individuals per species in each whole sample. The word “taxa” is used for the main sorted groups of invertebrates of different taxonomic ranks (phylum, class). Abundance refers to standardized values (ind./1,000 m²).

3. Results

The Vema-TRANSIT expedition with RV *Sonne* (SO-237) was the first expedition sampling benthic abyssal macrofauna along a latitudinal transect across the Vema Fracture Zone, North Atlantic (~11°N; Table 1) and in the Puerto Rico Trench by means of a C-EBS.

3.1. C-EBS deployment

The C-EBS was deployed with camera systems and CTD along the VFZ. The towing distance ranged between 602 and 2,020 m (Table 1). The oxygen concentration varied from 237.51 µM on the eastern side of the VFZ to 261.13 µM at the abyssal station in the PRT. The bottom water temperature showed an influence of the Antarctic bottom water on the western side of the VFZ where the water was slightly colder with 1.76 °C (station 11-4) compared to the MAR (station 8-4) with 1.81 °C and the eastern side of the VFZ with more than 2°C, for example 2.313°C at station 4-8. The bottom current velocities varied between 1.1 cm/s (station 2-7) and 6.58 cm/s (station 4-8) on the eastern side of the VFZ, 2.60 cm/s at the MAR (station 8-4) and between 2.58 cm/s (station 11-4) and 6.11 cm/s (station 9-2) on the western side of the VFZ. At the abyssal station 14-1 in the PRT the current velocity was 5.24 cm/s (Table 1).

The camera system did not work properly at all stations. Some sample pictures are presented in Figure 2 showing the seafloor at station 9-2 on the western side of the

VFZ when the C-EBS landed on the seafloor (Fig. 2 A, B) and the field of manganese nodules and rocks shortly before the EBS got stuck at this station (Fig. 2 C, D). The abyssal plain of the PRT was characterized by an even and flat topography with few shallow mounds and depressions (Fig. 2 E), while the eastern side of the VFZ (station 4-9) showed a number of “Lebensspuren” and a small hydromedusa (Fig. 2 F).

3.2. Faunistic composition

In total, 21,332 benthic macrofaunal invertebrate specimens were collected from the C-EBS (Table 2). Crustacea, Annelida and Mollusca occurred at all stations. Crustacea was the most abundant group in the material with 12,538 specimens (58,8%) followed by Annelida (mostly Polychaeta) with 5,491 specimens (25,7%), Mollusca with 1,458 specimens (6,8%), and Echinodermata with 778 specimens 3,6%), while Nematoda (502 specs. 2,4%), Chaetognatha (152 specs, 0,7%) and Porifera (131 specs, 0,6%) were less frequent. Rare taxa which occurred with less than ten individuals in the samples (< 0.1%) were Hemichordata, Phoronida, Priapulida, Brachiopoda, Chordata (2 appendicularian larvae), Echiurida, Komikiacea, Chelicerata and Platyhelmintes (Figure 3).

For comparability of abundances between stations, data of the taxa were normalized to 1,000 m trawled distances per station (Table 3) (Figures 4 A, B). Within the Crustacea, Peracarida with 7,848 individuals and Copepoda (Harpacticoida and Calanoida) with 4,526 individuals were dominating (Table 4). Ostracoda occurred with 145 individuals and were most prevalent on the eastern side of the VFZ, as were Eucarida which only occurred with 17 individuals). Only 1 specimen of Cirripedia was sampled at station 11-1 in the western abyssal basin of the VFZ.

Between the C-EBS stations, total abundances varied from 120 to 2,312 individuals/1,000 m^2 (Table 3, Figure 4 A, B). The lowest number of invertebrates was reported at station 11-4 with 120 individuals/1,000 m^2 at the western side of the VFZ. In the PRT we found the highest number of invertebrates at station 14-1 with 2,313 individuals/1000 m² at 4,552 m depth. The number of invertebrate taxa ranged between five (stations 12-5, 13-4, and 13-5 at hadal depths) and 14 (station 9-8) in the western abyssal basin of the VFZ (Figure 4 C).

Along the VFZ, abundances were generally higher at the stations of the eastern abyssal basin (502.7–1746.4 individuals/1000 m^2), than in the western abyssal basin (119.9–598.3 individuals/1000 m^2), but station 2-6 (east) showed a lower abundance (502.7 individuals/1000 m^2) than station 9-8 (west, 598.3 individuals/1000 m^2) (Figures 4A). Both, Crustacea and Annelida showed the highest abundances in PRT at station 14-1 (1591.6 and 489.5 individuals/1000 m^2, respectively), whereas Mollusca and Echinodermata in eastern VFZ at station 4-8 (153.1 and 129.1 individuals/1000 m^2, respectively). Nematoda showed the highest abundance also in the eastern VFZ at station 6-8 (85.0 individuals/1000 m^2). In general, abyssal abundances in the PRT were higher than in VFZ and the abundances of the hadal PRT stations are still higher than those of the abyssal VFZ in the western basin.

Relative abundances of taxa varied slightly between stations but at all stations 75% and more of relative abundances comprised only crustaceans and annelids (Figure 4b). Molluscs were the next abundant taxon at all stations, while notable relative abundances of other taxa varied: Echinoderms were notably better represented at sites 4, 12 and 14, poriferans at sites 9 and 11, and nematodes at stations 2-7 and 6-8.

The multivariate analysis of the higher taxon-assemblage structure of the Vema-TRANSIT stations showed significant separation of the hadal PRT stations and of the eastern VFZ from the western VFZ while the MAR and abyssal PRT stations grouped with the eastern VFZ (Figure 5 A, Supplement Table 1).

In order to test if the higher taxon-assemblage structures of the deep-water macrofauna collected at the Vema-TRANSIT stations were similar to those in other deep-water areas, they were compared with deep-water and abyssal only macrofauna EBS datasets from the North Pacific, South Atlantic, and Southern Ocean (Figure 5B). The deep-water MDS (Figure 5B) comprising EBS stations from 117 shelf to hadal depth of the Atlantic, Pacific and Southern oceans showed a complex 2-D plot with a high stress while the ANOSIM documented significances for factors depth, region and area of the entire dataset. (Fig. 5B) To further investigate the higher taxon-assemblage structure at abyssal depth, only stations from this depth zone were included in the following analysis (Figure 5C). The resulting 2D graph (stress 0.13) showed an apparent separation of the abyssal station of the Sea of Japan. Pairwise tests of significance only showed significant separations in abyssal higher macrofaunal taxon assemblage structure between some regions but not between areas (Supplement Tables 2, 3).

4. Discussion

4.1. C-EBS deployment

The VFZ has been sampled for the first time using a C-EBS, however, Robertson (2013) sampled the seamount tops at some stations of the western side of the VFZ using ROVs and reported especially on corals. At hadal depths > 8000 m a fine meshed epibenthic sledge was deployed for the first time in deep-sea research in the PRT. The handling of the sampling gear can have implications on the capture of the less frequent animals (e.g. sponges) (Janussen and Tendal, 2007). In the deep sea, especially at abyssal and hadal depths, tiny macrofaunal sponges, such as species of the Cladorhizidae (e.g. *Asbestopluma* Topsent, 1901) and Calcarea, were more frequently collected with the EBS than by larger mesh-sized bottom trawls like the Agassiz trawl (Janussen, personal communication). No box corers were deployed for catching macrofaunal invertebrates in the VFZ. Moreover, is gear also collects a different faunal fraction if compared to the epibenthic sledge (Brandt and Schnack, 1999). Therefore we primarily focused on the discussion of comparable EBS samples in the following. For this gear the catch of fast swimming animals (e.g. decapod shrimps) is problematic. Nevertheless, some of vagile animals usually get caught and have been documented by pictures (Figure 2 A, B), but in general, Eucarida are underrepresented in the samples (Table 4) compared to peracarid and copepod crustaceans.

Sediments at abyssal depths of around 5,000 m were fine and silty (Devey et al., this volume, Linse et al., this volume), especially at the eastern side of the VFZ, what was possibly a reason why we found more crustaceans here compared to the western side of the VFZ. The benthic habitats in the east did not contain manganese nodules, while the habitats sampled in the West contained a huge number of nodules or manganese crust (figure 2C, D). Furthermore, the temperature differed along the VFZ. It was colder on the western side of the VFZ than on the eastern side, indicating an influence of the cold Antarctic bottom water extending north (e.g. Rintoul et al., 2001, 2012; Reid, 1996) and possibly causing faunal similarities between the fauna of the western VFZ and that of areas further in the southwest of the Atlantic or even the Southern Ocean Weddell Sea.

4.2 Faunistic composition

Numbers of specimen sampled in our study appear to be low for some stations in the western abyssal basin and at the hadal stations in the Puerto Rico trench. The abundance of macrobenthic taxa decreased with depth, a phenomenon already described before (Dahl, 1954, Hessler and Sanders, 1967, Gage and Tyler, 1991). For hadal depths, however, abundance data are scarce and usually refer to material collected by means of baited traps (e.g. Jamieson, 2015).

A comparison of the fauna of both sides of the VFZ documented higher abundances in the eastern basin compared to the western basin (Tables 2-4, Figure 4 A) while numbers of taxa sampled were more or less equal on both sides, except for station 9-8 where we found the highest number of taxa (Figure 4 C). Abundances of the hadal PRT stations were higher than those of the western abyssal basin of the VFZ, except for station 9-8 which had almost as high abundances as station 12-6. In general, relative abundance of Crustacea was higher at the hadal stations of the PRT while that of Annelida (mainly Polychaeta) was lower than along the VFZ (Figure 4 B). Within the Peracarida, Isopoda were most frequent at these stations, while studies of abundances of macrofaunal crustaceans from the Atlantic sector of the Southern Ocean (e.g. De Broyer and Jazdzewski, 1996) showed somewhat different patterns with Amphipoda dominating, but these data refer to shallower depths. Within the Polychaeta the hadal stations were slightly different in family composition to the abyssal areas (Guggolz et al., this volume).

The differences in the abundances between the eastern and western side of the VFZ might be explained by the differences in the environmental settings in terms of sediments on both sides of the MAR (Devey et al., this volume). The sediments on the western side were characterized by either manganese crust where polychaetes thrived better than at stations with larger manganese nodules (Guggolz et al., this volume) or even by large manganese nodules of up to 10 cm in diameter (station 9-2), forming hard structures below the thin sediment layer (Devey et al., this volume; Figure 2 A-D) potentially providing sessile fauna substrate for settling. The substrate type as well as the environmental variables (e.g. temperature, salinity) could be a driving factor influencing the abundance of poriferans in the western basin compared to the eastern basin (Figure 2 F) where suitable hard substratum for sessile organisms was limited but instead soft bottom dominated. Besides lower abundances of soft sediment dwellers due to the smaller proportion of their preferred habitat, the abundant hard substratum may have furthermore had an impact on the performance of the C-EBS and thus caused a sampling bias.

The multivariate analysis showed that the hadal stations of the PRT were different from all other stations in general macrofaunal composition (Figure 5 A), and that the macrofaunal composition of the eastern and western sides of the VFZ in general showed a separation from each other, despite station 6-7 from the eastern VFZ grouping within the western VFZ group . Abyssal stations of the PRT, however, showed similarities to the stations of the western VFZ as well as to station 8-4 from the MAR (Figure 5 A). As the Antarctic Bottom Water might influence life on the seafloor and support dispersal of species, we also compared our macrofaunal data with those from the Southern Ocean shelf and slope from a previous expedition. Moreover, we included data from other Atlantic and Pacific basins and could demonstrate that the samples from the Southern Ocean shelf and slope were very different to all other stations in macrofaunal composition and so were stations from bathyal depth of the northwest Pacific, however, some stations from abyssal depths of the northwest Pacific were similar to those of the abyssal PRT, eastern and western side of the VFZ as well as the abyssal stations of the southwest Atlantic (Figure 5 B). For this reason we compared only abyssal stations of these areas (Figure 5 C). The abyssal stations of the Sea of Japan were clearly different in macrofaunal composition to all other stations, those from the Kuril-Kamchatka abyssal plain, however, were similar to stations on both sides of the VFZ, as well as the Argentine and Brazilian basins (Brix, pers. comm., unpublished). A clear pattern, however, could not be observed at the level of macrofaunal composition, possibly indicating the importance of working at lower taxon level, such as family, genus or even better species level. Differences between western and eastern side of the VFZ have to be expected at species level as life styles within a higher taxon are very variable and diverse. Moreover species or individuals react to and adapt to the environment and not higher taxa. However, a few examples documenting differences in species, genus or family composition of selected abundant macrofaunal taxa were referred to in detail in some of the papers of the present issue (e.g. Bober et al., this volume, Guggolz et al., this volume, Linse & Schwabe, this volume, Riehl et al., this volume). The purpose of this paper, however, was to present a general composition in order to document all taxa sampled during this expedition.

In the Atlantic sector of the Southern Ocean the overall taxon composition in EBS samples collected in the continental shelf depth (200 m - <1000 m) during the BIOPEARL I expedition (Linse, 2006) showed Crustacea as the most common taxon with 39 % followed by Mollusca (30%), Annelida (16%) and Echinodermata (4 %), a pattern that changed only slightly in the upper bathyal to Crustacea 42%, Annelida 25%, Mollusca 10 % and Echinodermata 5% (Linse, unpublished data). This overall composition of macrofaunal taxa sampled by EBS resembled the one seen in the current study (Fig. 3) and is in support with the view that the Antarctic and deep sea benthic faunas share characteristics. Abundances in these shelf EBS samples were higher than those in the Vema TRANSIT samples but this can be explained by the higher food supply on the shelf compared to the abyssal deep sea.

Further north, in the South Polar Front (SPF) abundance data of macrofaunal benthic taxa sampled with an epibenthic sledge were magnitudes lower than in the Southern Ocean Weddell Sea (Brandt et al., 2007, 2012, 2014) and also in the VFZ. In the SPF, also Crustaceans dominated the macrofaunal assemblages at the stations followed by Annelida (Polychaeta) and Mollusca (Brandt et al., 2014). In this area isopod crustaceans were the dominant peracarid taxon (Meyer-Löbbecke et al., 2014). This and other peracarid taxa yielded much higher numbers of individuals in the Beagle Channel, however, from much shallower stations from the shelf (25 m) to the deep sea (663 m) with 104,618 peracarids (55,633 ind./1,000 m^2), 15,025 amphipods, and 2,454 tanaids (Brandt et al., 1997; 1998).

In the Pacific, macrofauna was collected in the Sea of Japan by means of the C-EBS (Brandt et al., 2013). Here also Crustacea yielded the highest abundance followed by Annelida and Mollusca (Brandt et al., 2013), contrary to the open Abyssal plain adjacent to the Kuril-Kamchatka Trench where abundances of Annelida were almost as high as those of the Crustacea (Brandt et al., 2015). Macrofauna abundance, species diversity and turnover has been investigated at three sites in the Clipperton-Clarion Fracture Zone (Wilson, 2017). This author documented that macrofauna densities varied with productivity, but was not consistent amongst macrofaunal groups. Species diversities of Polychaeta, Isopoda and Tanaidacea showed different trends in relation to export productivity. Polychaeta had the highest estimated species diversity at the high-productivity site and the lowest values at the low-productivity site Tanaidacea showed a similar pattern, Isopoda the opposite trend.

The results of this study showed that in general terms the macrofaunal composition of abyssal areas is usually dominated by Crustacea, followed by Annelida and Mollusca. Differences in percentages of occurrence seem to depend on environmental factors or may be a result due to intra- or interspecific taxon competition.

The lack of a clear separation of eastern and western VFZ macrofauna compositions showed that the MAR does probably not act as a barrier separating entire faunae. Differences observed were furthermore likely influenced by different environmental settings and performance of the collection gear. Studies investigating species distribution across the MAR in macrostylid isopods, however, highlight the potential barrier effect the MAR may have on certain taxa (Bober et al., this volume). Nevertheless, it remains difficult to distinguish between barrier effects of the MAR and those of geographic distance in supposedly poor dispersers (Riehl et al., this volume).

While the outstanding pattern observed in the PRT may be attributed partly to the peculiar sediment observed there, patterns of genetic-distance distribution and molecular operational taxonomic units (MOTU) distribution observed in target taxa (e.g. macrostylid isopods) supported our find of a distinct fauna. The occurrence of certain dominant macrofaunal species at the PRT bottom (Kniesz et al, this volume) while other species were shared between hadal and adjacent abyssal (Riehl et al., this volume) indicated particular environmental conditions (including depth-related factors) influencing the evolution of a distinct trench fauna.

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Table 1. Characteristic of the stations sampled by means of a C-EBS during Vema-TRANSIT expedition. E VFZ: eastern Vema Fracture Zone, MAR: Mid Atlantic Ridge, W VFZ: western Vema Fracture Zone, PRT: Puerto Rico Trench; a: off deck; b: calculated by distance; c: calculated by flowmeter measure; O2, Temperature and Current data provided by CTD fit in the C-EBS; -: not available data.

Station	Area	Date	Hour [a]	Coordinates				Depth max.	Towing distance [b]	O_2	Temp	Current
				start ship position		end ship position		[m]	[m]	[µM]	[°C]	[cm/s]
2-6	E VFZ	20/12/14	7:52	10° 43.17' N	25° 04.49' W	10° 43.80' N	25° 03.73' W	5520	1846	237.5	2.30	1.7
2-7	E VFZ	20/12/14	16:30	10° 42.06' N	25° 04.26' W	10° 42.94' N	25° 03.16' W	5507	2020	238.2	2.29	1.1
4-8	E VFZ	26/12/14	21:59	10° 24.96' N	31° 05.19' W	10° 25.63' N	31° 04.38' W	5725	1750	238.3	2.31	6.6
4-9	E VFZ	27/12/14	6:55	10° 24.94' N	31° 03.83' W	10° 25.67' N	31° 02.98' W	5733	1900	238.0	2.31	2.0
6-7	E VFZ	02/01/15	14:38	10° 21.33' N	36° 55.93' W	10° 21.84' N	36° 55.06' W	5079	1980	245.8	2.29	2.4
6-8	E VFZ	02/01/15	23:12	10° 22.25' N	36° 56.05' W	10° 22.66' N	36° 55.35' W	5127	1400	245.4	2.21	2.1
8-4	MAR	06/01/15	15:45	10° 43.00' N	42° 40.67' W	10° 43.01' N	42° 39.73' W	5178	1750	239.1	1.81	2.6
9-2	W VFZ	11/01/15	7:41	11° 40.58' N	47° 58.93' W	11° 40.45' N	47° 59.00' W	4986	673[c]	240.9	1.79	6.1
9-8	W VFZ	12/01/15	15:12	11° 39.21' N	47° 54.96' W	11° 39.37' N	47° 53.98' W	5001	1613	241.6	1.80	2.2
11-1	W VFZ	14/01/15	6:16	12° 05.76' N	50° 28.85' W	12° 05.81' N	50° 27.96' W	5088	1320	239.2	1.76	4.9

11-4	W VFZ	14/01/15	15:08	12° 04.76' N	50° 28.94' W	12° 04.83' N	50° 28.14' W	5108	1416	239.4	1.76	2.6
12-5	PRT	20/01/15	19:56	19° 46.50' N	66° 50.97' W	19° 46.85' N	66° 49.99' W	8338	1611	-	-	-
12-6	PRT	21/01/15	3:26	19° 48.49' N	66° 45.44' W	19° 48.61' N	66° 45.11' W	8336	602	-	-	-
13-4	PRT	23/01/15	3:00	19° 46.73' N	67° 06.21' W	19° 47.13' N	67° 05.79' W	8317	750	-	-	-
13-5	PRT	23/01/15	12:05	19° 49.85' N	67° 02.91' W	19° 50.14' N	67° 02.60' W	8042	840	-	-	-
14-1	PRT	24/01/15	16:35	19° 01.63' N	67° 09.73' W	19° 02.11' N	67° 09.43' W	4552	764	261.1	2.25	5.3
14-2	PRT	24/01/15	22:23	19° 04.16' N	67° 08.11' W	19° 04.67' N	67° 07.75' W	4925	968	257.7	2.24	2.1

Table 2: Raw presence data of invertebrate taxa of the Vema-TRANSIT stations.

	Area	eastern VFZ						MAR	western VFZ				PRT						
	Stations	2-6	2-7	4-8	4-9	6-7	6-8	8-4	9-2	9-8	11-1	11-4	12-5	12-6	13-4	13-5	14-1	14-2	
Taxa	Depth (m)	5520	5507	5725	5733	5079	5127	5178	4986	5001	5088	5108	8338	8336	8317	8042	4552	4925	Total
Annelida		275	804	697	977	376	607	391	24	206	59	51	48	84	36	40	374	442	5491
Brachiopoda		-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	2
Bryozoa		-	-	-	-	6	1	-	-	6	5	-	-	-	-	-	-	-	18
Chaetognatha		4	28	31	18	9	15	15	2	6	7	-	2	-	4	-	3	8	152
Chelicerata		-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Chordata		-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	2
Cnidaria		-	14	6	2	4	30	7	-	4	4	3	-	-	-	-	1	3	78
Crustacea		586	1543	1752	1793	930	1058	725	83	559	100	80	406	275	313	247	1216	872	12538
Echinodermata		12	62	226	236	10	13	8	-	31	-	2	42	20	12	4	45	55	778
Echiura		-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2
Foraminifera		-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	2
Hemichordata		1	4	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	7
Mollusca		22	159	268	220	96	135	81	8	48	17	20	64	19	52	27	105	117	1458
Nematoda		16	130	29	63	26	119	20	4	28	8	1	0	1	0	1	14	42	502
Nemertea		1	6	2	1	10	8	-	1	4	1	-	-	1	-	-	-	-	35
Phoronida		-	2	-	-	-	2	-	-	-	-	-	-	-	-	-	2	1	7
Platyhelminthes		2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Porifera		6	9	4	1	4	3	1	8	49	6	8	-	2	-	-	6	24	131

Priapulida	-	5	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	7
Sipunculida	2	13	2	6	18	24	8	2	21	5	5	-	-	-	-	-	2	108
Indet.	1	4	-	-	-	-	1	4	-	1	-	-	-	-	-	-	-	11
Total	928	2783	3018	3318	1489	2016	1258	139	965	214	170	562	403	417	319	1767	1566	21332

Table 3: Abundance data (individuals/1000 m²) of macrofauna of the Vema-TRANSIT stations.

	Area	eastern VFZ						MAR	western VFZ				PRT					
	Stations	2-6	2-7	4-8	4-9	6-7	6-8	8-4	9-2	9-8	11-1	11-4	12-5	12-6	13-4	13-5	14-1	14-2
Taxa	Depth (m)	5520	5507	5725	5733	5079	5127	5178	4986	5001	5088	5108	8338	8336	8317	8042	4552	4925
Annelida		149.0	398.0	398.3	514.2	189.9	433.6	223.4	30.5	127.7	44.7	36.0	29.8	139.5	48.0	47.6	489.5	456.6
Brachiopoda		-	-	-	-	-	-	-	1.3	0.6	-	-	-	-	-	-	-	-
Bryozoa		-	-	-	-	3.0	0.7	-	-	3.7	3.8	-	-	-	-	-	-	-
Chaetognatha		2.2	13.9	17.7	9.5	4.5	10.7	8.6	2.5	3.7	5.3	-	1.2	-	5.3	-	3.9	8.3
Chelicerata		-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-
Chordata		-	-	-	0.5	-	-	-	-	-	0.8	-	-	-	-	-	-	-
Cnidaria		-	6.9	3.4	1.1	2.0	21.4	4.0	-	2.5	3.0	2.1	-	-	-	-	1.3	3.1
Crustacea		317.4	763.9	1001.1	943.7	469.7	755.7	414.3	105.6	346.6	75.8	56.5	252.0	456.8	417.3	294.0	1591.6	900.8
Echinodermata		6.5	30.7	129.1	124.2	5.1	9.3	4.6	-	19.2	-	1.4	26.1	33.2	16.0	4.8	58.9	56.8
Echiura		-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	1.3	-
Foraminifera		-	-	-	-	-	0.7	-	1.3	-	-	-	-	-	-	-	-	-
Hemichordata		0.5	2.0	-	-	-	-	0.6	-	-	-	-	-	1.7	-	-	-	-
Mollusca		11.9	78.7	153.1	115.8	48.5	96.4	46.3	10.2	29.8	12.9	14.1	39.7	31.6	69.3	32.1	137.4	120.9
Nematoda		8.7	64.4	16.6	33.2	13.1	85.0	11.4	5.1	17.4	6.1	0.7	-	1.7	-	1.2	18.3	43.4
Nemertea		0.5	3.0	1.1	0.5	5.1	5.7	-	1.3	2.5	0.8	-	-	1.7	-	-	-	-
Phoronida		-	1.0	-	-	-	1.4	-	-	-	-	-	-	-	-	-	2.6	1.0
Platyhelminthes		1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porifera		3.3	4.5	2.3	0.5	2.0	2.1	0.6	10.2	30.4	4.5	5.6	-	3.3	-	-	7.9	24.8
Priapulida		-	2.5	-	-	-	-	-	1.3	0.6	-	-	-	-	-	-	-	-

Sipunculida	1.1	6.4	1.1	3.2	9.1	17.1	4.6	2.5	13.0	3.8	3.5	-	-	-	-	-	2.1
Indet.	0.5	2.0	-	-	-	-	0.6	5.1	-	0.8	-	-	-	-	-	-	-
Total	502.7	1377.9	1724.4	1746.4	752.0	1439.8	719.0	176.9	598.3	162.3	119.9	348.8	669.5	555.9	379.7	2312.7	1617.8

Table 4: Crustacea of the Vema-TRANSIT stations.

area	Veast	Veast	Veast	Veast	Veast	Veast	MAR	Vwest	Vwest	Vwest	Vwest	PRT	PRT	PRT	PRT	PRT	PRT	
Crustacea	2-6	2-7	4-8	4-9	6-7	6-8	8-4	9-2	9-8	11-1	11-4	12-5	12-6	13-4	13-5	14-1	14-2	Total
Peracarida	182	698	808	861	662	602	480	57	442	78	64	382	273	306	240	973	740	7848
Eucarida	0	3	4	3	1	1	0	0	0	1	1	0	0	0	1	0	2	17
Cirripedia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Ostracoda	4	36	16	28	10	29	8	1	5	2	2	2	0	0	0	1	1	145
Copepoda	400	806	924	900	257	426	237	25	112	18	13	22	2	7	6	242	129	4526

Figure 1: Sites sampled across the Vema-Fracture Zone and in the Puerto Rico Trench (Map: courtesy of Nico Augustin).

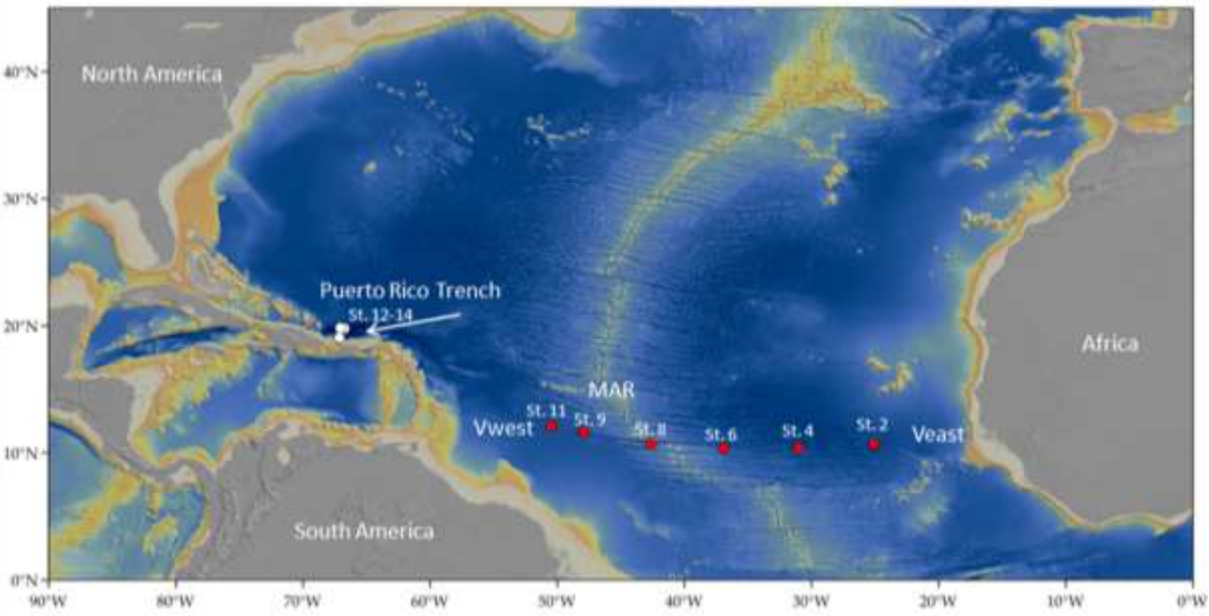


Figure 2 (For figure legend, see figure caption).

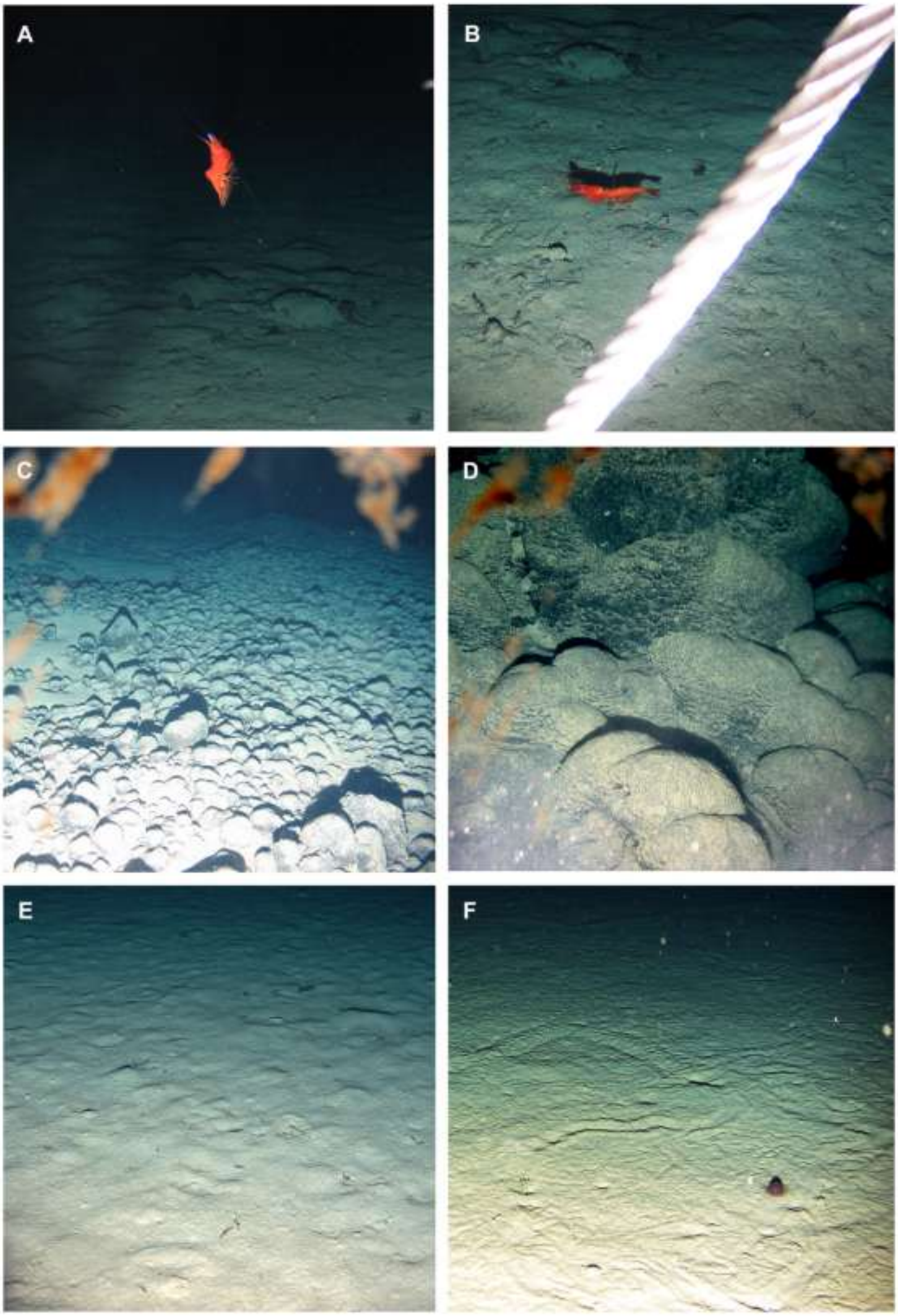


Figure 3: Global composition of the macrofauna sampled by means of a C-EBS during the Vema-TRANSIT expedition. Others: taxa which contribute with less than 0.5% to the total individuals; i.e. Sipunculida, Cnidaria, Nemertea, Bryozoa, Priapulida, Phoronida, Hemichordata, Plathyelmintha, Brachiopoda, Chordata, Chelicerata).

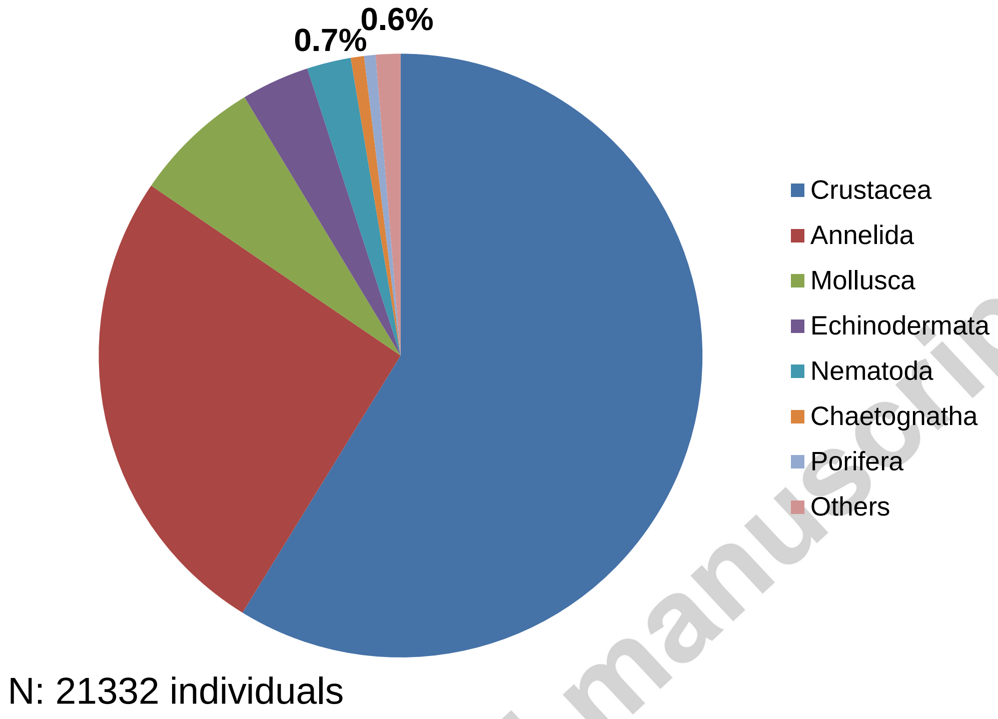


Figure 4: A: Abundance (ind./1000 m2) of macrofauna sampled by means of a C-EBS at each station during the Vema-TRANSIT expedition. Others = taxa occurring with less than 10 individuals in the samples (Hemichordata, Phoronida, Priapulida, Brachiopoda, Chordata, Echiurida, Foraminifera, Chelicerataa, Plathelminthes, indet).

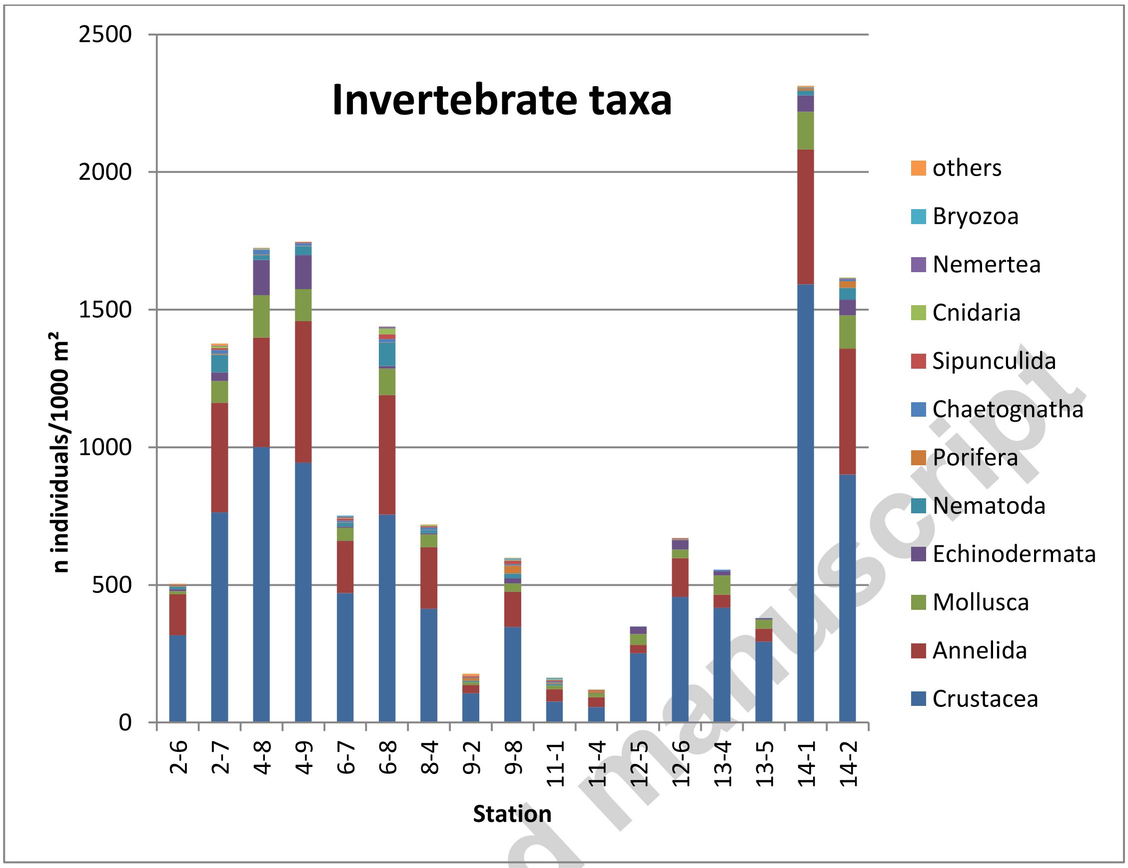


Figure 4B: Relative abundance of macrofauna.

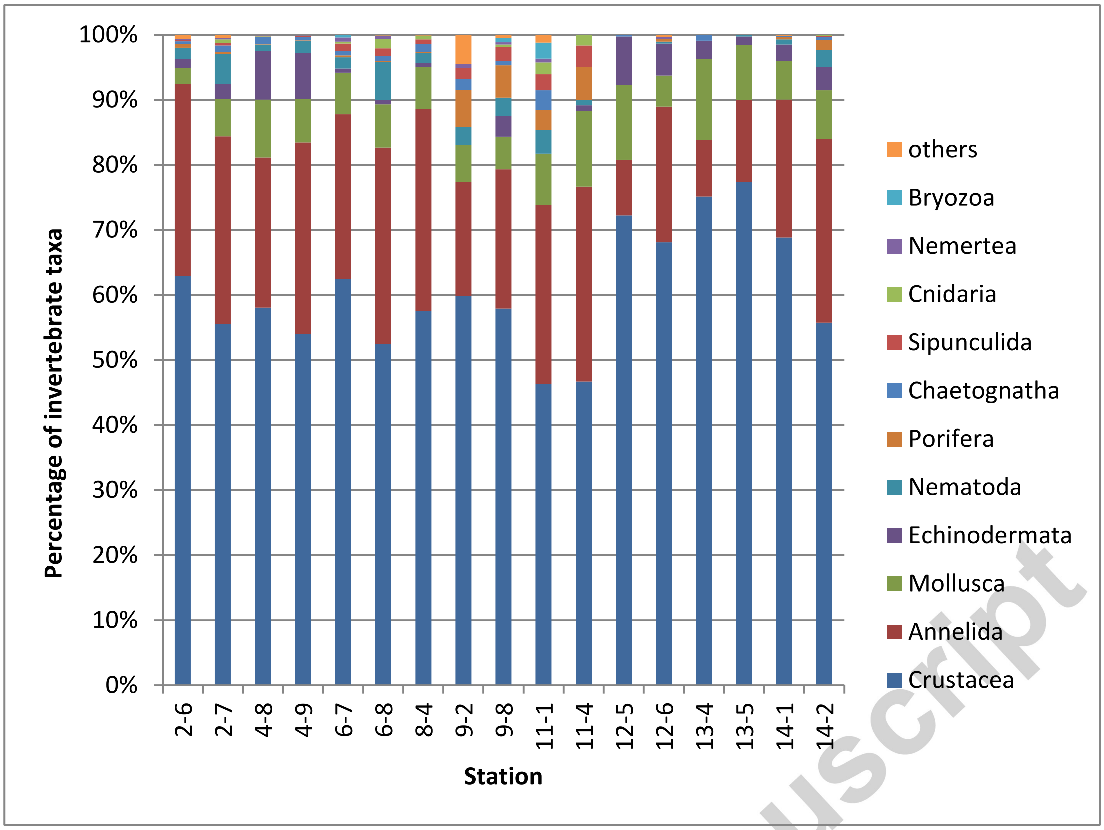


Figure 4 C: Number of macrofaunal taxa identified at Vema-TRANSIT stations.

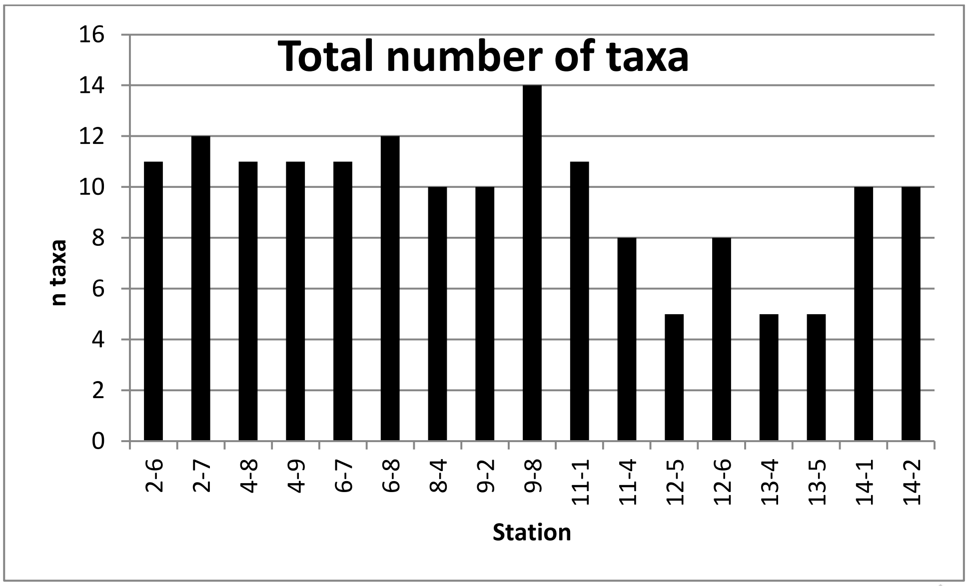
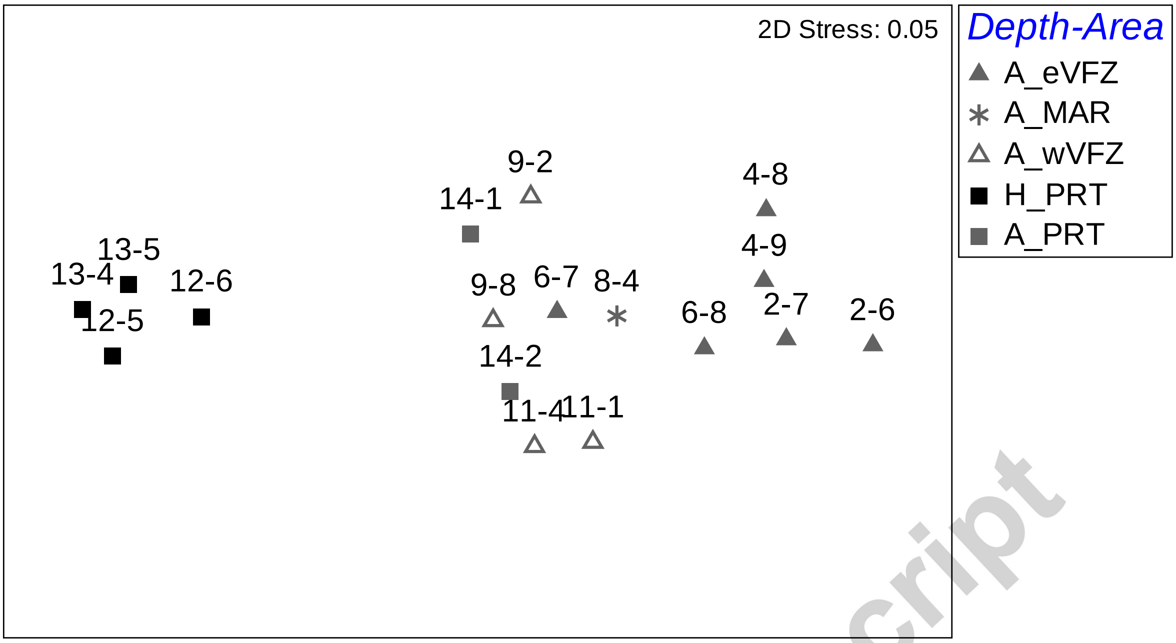
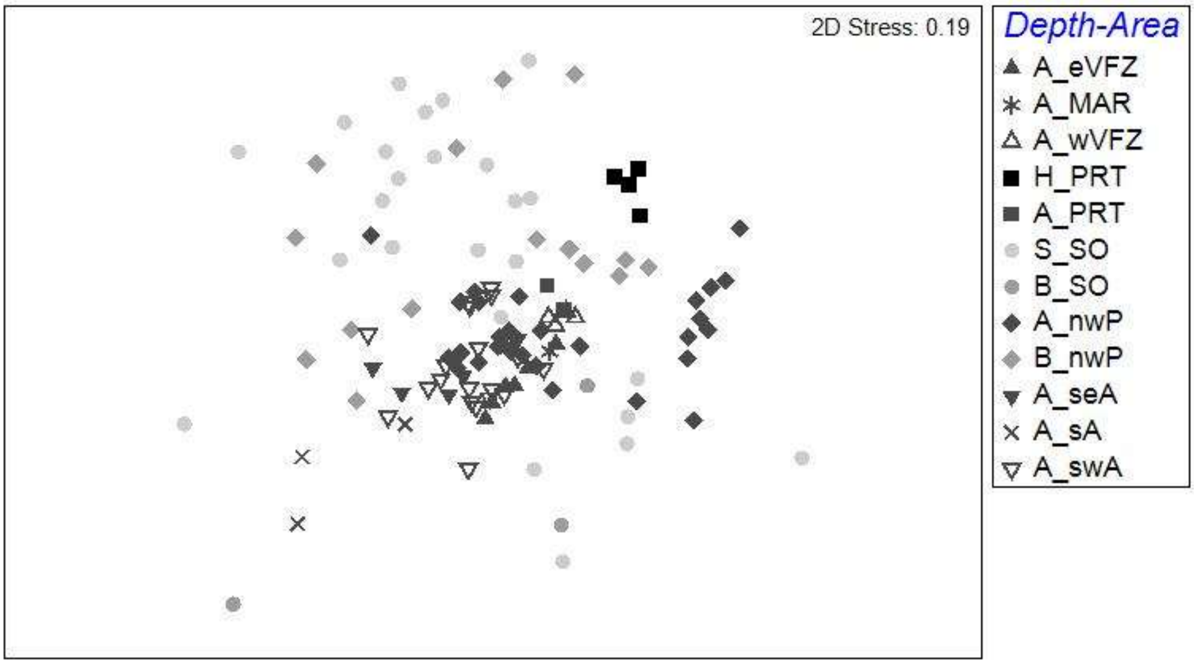


Figure 5 A: MDS of standardized Bray-Curtis similarities from VEMA TRANSIT datasets (for abbreviations see 2.6).



Abbreviations: A_eVFZ – Abyssal eastern basin Vema-Fracture Zone, A_MAR – Abyssal Mid-Atlantic Ridge, A_nwP – Abyssal northwestern Pacific, A_PRT – Abyssal Puerto Rico Trench, A_wVFZ – Abyssal western basin Vema-Fracture Zone.

Figure 5 B: nMDS of standardized Bray-Curtis similarities from multiple EBS macrofauna datasets (for abbreviations see 2.6).



Abbreviations: A_eVFZ – Abyssal eastern basin Vema-Fracture Zone, A_MAR – Abyssal Mid-Atlantic Ridge, A_nwP – Abyssal northwestern Pacific, A_PRT – Abyssal Puerto Rico Trench, A_sA – Abyssal southern Atlantic, A_seA – Abyssal southeastern Atlantic, A_swA – Abyssal southwestern Atlantic, A_wVFZ – Abyssal western basin Vema-Fracture Zone, B_nwP – Bathyal northwestern Pacific, B_SO – Bathyal Southern Ocean, H_PRT – Hadal Puerto Rico Trench, S_SO – Shelf Southern Ocean.

Figure 5 C: nMDS of standardized Bray-Curtis similarities from multiple abyssal EBS macrofauna datasets (for abbreviations see 2.6).

Abbreviations: Aghulas B – Aghulas Basin, Ango B – Angolas Basin, Arg B – Argentine Basin, Braz B – Brazilian Basin, Cape B – Cape Basin, eVFZ – eastern basin Vema-Fracture Zone, Guin B – Guinea Basin, KKT – Kurielen Kamchatka Trench, MAR –Mid-Atlantic Ridge, PRT –Puerto Rico Trench, sMAR – southern Mid Atlantic Ridge, SoJa – Sea of Japan, wVFZ – western basin Vema-Fracture Zone.