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Harpacticoida (Crustacea, Copepoda) across a longitudinal transect of the Vema Fracture Zone and along a depth gradient in the Puerto Rico trench

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ABSTRACT

The aim of this study was the investigation of abundance, composition and biodiversity of benthic deep-sea Harpacticoida (Crustacea, Copepoda) in the Vema Fracture Zone (VFZ) and Puerto Rico trench. The study revealed a clear East-West gradient in total abundance of Harpacticoida with a westward decrease in abundances in the VFZ and significant differences in the community composition in the Eastern (East Vema) and Western Atlantic basin (West Vema) on family and genus level. The Puerto Rico trench and its upper slope did not only differ in abundance, but were distinct with respect to community composition on family and genus level. Thus, the upper slope might be considered as an ecotone, a transition zone where a rapid distinction of species composition occurs. In our study fiarea, 837 adult harpacticoid specimens could be assigned to 16 families and 1 subfamily. The most abundant families found were Ameiridae Boeck, 1865, Pseudotachidiidae Lang, 1936 and Ectinosomatidae Sars, 1903. Genera and species were investigated within selected families (Argestidae Por, 1986, Cletodidae T. Scott, 1905, Canthocamptidae Brady, 1880 and Zosimeidae Seifried, 2003) where 11 genera, and 73 species could be discriminated. Within the selected families, the genera *Zosime* Boeck, 1873 and *Mesocletodes* Sars, 1909 were dominant. In the study area, a high number of singletons was detected, which might be endemic to the respective region. Furthermore, a low total number of species in the trench was observed which was attributed to frequent disturbances in the dynamic environment of the Puerto Rico trench (e.g. turbidites or seismic activity) and high adaptability of specialists and opportunists to these disturbances.

1. Introduction

In addition to the vast number of continental slopes and basins in the deep sea, other geological structures, such as mid-oceanic ridges and hadal trenches, exist (Ramirez-Llodra et al., 2010).

The Mid-Oceanic Ridge (MOR), a marine mountain chain, forms boundaries between two adjacent plates and is considered one of the most striking structures covering a large part of ocean basins. The global MOR system measures approximately 75,000 km (Garrison, 1993; Macdonald and Fox, 1990; Tardent, 2005) and covers 33% of the surface area of the seabed (Gage and Tyler, 1991; Tardent, 2005). The Mid-Atlantic Ridge (MAR), as part of the global ridge system, divides the Atlantic Ocean into Eastern and Western basins and is interrupted by a number of fracture zones with the Vema Fracture Zone (VFZ) being one of the largest fracture zones in the equatorial Atlantic (Auzende et al., 1990; Devey, (this issue), this volume, Levin and Gooday, 2003).

Fracture zones have been created through the displacement of the MOR by transform faults which occur exclusively on plate boundaries and terminate where they meet the offset which they connect. A fracture zone is thus an extension of a transform fault outside of two successive ridge segments (e.g. Hekinian, 2014; Macdonald and Fox, 1983, 1990; Sandwell, 1984; Şengör, 2014). The offset of the MAR allows the bottom water to flow from one side of the ocean to the other (Morozov et al., 2010, 2015). Besides fracture zones, other significant geological structures in the deep sea are trenches, which represent long, narrow and steep depressions at subduction zones. A deep-sea trench begins at a depth of 6500 m (Jamieson, 2015; Watling et al., 2013) and can reach depths of 11,000 m, thus representing the deepest parts of the ocean (Gardner et al., 2014; Jamieson, 2015). Although trenches are considered extreme marine ecosystems with high hydrostatic pressure and geological instability, a high biodiversity is found here (Jamieson, 2015). Trenches are subject to frequent disturbances (landslides,

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Table 1

Sampling details of the Vema-TRANSIT expedition in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic per MUC haul (denotations of hauls was generated by order of gears) sampling date (UTC), coordinates and measured environmental variables: depth (m), total organic matter = TOM (%), total nitrogen = TN (%), total organic carbon = TOC (%) and grain size variable: volume weighted mean D [4, 3].

Stat-ion	Haul	Date	Latitude	Longitude	Regions	Depth	TOM	TN	TOC	D [4, 3]
A1	2–3	19–12–14	10°43,112'N	25°3886'W	East-Vema-Abyssal	5498.0	7.43	0.15	0.70	41.11
A1	2–4	19–12–14	10°43,108'N	25°3888'W	East-Vema-Abyssal	5507.0	9.83	0.24	0.82	39.02
A1	2–5	20–12–14	10°43,17'N	25°3,88'W	East-Vema-Abyssal	5508.0	9.33	0.24	0.85	32.59
A3	6–3	01–01–15	10°21,03'N	36°57,59'W	East-Vema-Abyssal	5137.0	8.22	0.15	0.60	25.79
A3	6–4	02–01–15	10°21,03'N	36°57,61'W	East-Vema-Abyssal	5137.4	9.15	0.16	0.62	26.67
A3	6–5	02–01–15	10°21,03'N	36°57,61'W	East-Vema-Abyssal	5136.1	8.84	0.15	0.60	27.78
A4	8–2	06–01–15	10°43,562'N	42°41,593'W	Central-Vema-Abyssal (transform fault)	5182.2	12.41	0.19	0.76	18.61
A4	8–10	08–01–15	10°42,58'N	42°40,99'W	Central-Vema-Abyssal (transform fault)	5117.0	10.45	0.44	0.69	29.32
A4	8–11	08–01–15	10°42,59'N	42°40,99'W	Central-Vema-Abyssal (transform fault)	5121.9	9.36	0.15	0.60	31.80
B1	9–3	11–01–15	11°41,37'N	47°57,36'W	West-Vema-Abyssal	4999.0	9.62	0.12	0.50	43.83
B1	9–4	12–01–15	11°41,36'N	47°57,34'W	West-Vema-Abyssal	4998.3	8.01	0.10	0.47	40.96
B2	11–5	14–01–15	12°5,40'N	50°26,98'W	West-Vema-Abyssal	5090.7	6.29	0.12	0.49	60.35
B2	11–6	15–01–15	12°5,42'N	50°26,98'W	West-Vema-Abyssal	5091.5	5.81	0.14	0.43	68.43
B2	11–7	15–01–15	12°5,40'N	50°26,97'W	West-Vema-Abyssal	5091.4	6.01	0.12	0.47	75.15
C1	12–3	20–01–15	19°46,01'N	66°50,00'W	Puerto-Rico trench	8336.3	8.36	0.21	0.94	16.50
C1	12–7	21–01–15	19°46,004'N	66°49,990'W	Puerto-Rico trench	8337.6	6.63	0.18	0.78	16.03
C1	12–8	21–01–15	19°45,998'N	66°49,995'W	Puerto-Rico trench	8339.6	9.03	0.18	0.80	17.53
C2	13–1	22–01–15	19°43,809'N	67°9284'W	Puerto-Rico trench	8349.1	7.41	0.17	0.75	16.89
C2	13–2	22–01–15	19°43,812'N	67°9284'W	Puerto-Rico trench	8347.8	6.52	0.22	0.77	16.05
C2	13–3	22–01–15	19°43,817'N	67°9285'W	Puerto-Rico trench	8346.7	6.57	0.16	0.72	13.96
C3	14–3	25–01–15	19°4,68'N	67°7,77'W	Upper slope of the Puerto Rico trench	4924.9	8.58	0.17	0.62	49.06
C3	14–4	25–01–15	19°4,66'N	67°7,75'W	Upper slope of the Puerto Rico trench	4924.8	8.51	0.16	0.64	60.55
C3	14–5	25–01–15	19°4,66'N	67°7,76'W	Upper slope of the Puerto Rico trench	4925.0	8.13	0.17	0.61	57.95

earthquakes, currents), which might be important for the distribution of sediment-dwelling meiofauna that are, for instance, swept away by currents and recolonize sediments elsewhere (Jamieson, 2010, 2015; Oguri et al., 2013). However, trenches are among the least studied deep-sea habitats and control mechanisms for the distribution and variation of communities over time are poorly understood (Ichino et al., 2015; Jamieson, 2015).

Meiofauna are the most abundant metazoans in marine sediments (Giere, 2009) and show a cosmopolitan distribution (Bhadury et al., 2008; Coomans, 2000; Derycke et al., 2008). Following Nematoda harpacticoid Copepoda is the most common meiofaunal taxon in the benthos. They can inhabit a variety of habitats as reflected by their diverse body shapes and morphology (Higgins and Thiel, 1988; Huys and Boxshall, 1991; Giere, 2009). All of these characteristics make Copepoda suitable for studies dealing with abundance, community structure and distribution patterns in the deep sea. There are indeed many theories about the general modes of distribution of meiofauna including passive distribution by resuspension (Bell and Sherman, 1980; Wainright, 1990) or adhesion to marine snow (Shanks and Edmondson, 1990) or plants and plastic particles, which are relocated by currents and benthic storms (Alldredge and Silver, 1988; Alve, 1999; Winston, 2012). Some taxa, including harpacticoid Copepoda species, are able to leave the sediment ('emergers') and actively swim in the water column (Thistle, 2003; Thistle and Sedlacek, 2004). Despite this capacity for dispersion, until recently it was assumed that geological formations can act as physical barriers for the distribution of deep-sea meiofauna (Gage and Tyler, 1991). Recent studies however showed that, for some taxa, either no such barriers exist or that they only limit species distribution (Lins et al., in this issue; Menzel et al., 2011). For instance, species of the harpacticoid genus *Mesocletodes* Sars (1909) and Paramesochridae Lang, 1944 (Gheerardyn and Veit-Köhler, 2009; Menzel et al., 2011) do not seem to be restricted in their geographic distribution by either topography or distance.

Although a long research tradition exists in the Northeast Atlantic, only a few morphology-based biodiversity analyses of Harpacticoida have been carried out so far in the Northeast and Northwest Atlantic (Baguley et al., 2006; Chertoprud et al., 2010; George and Schminke, 2002; Gheerardyn et al., 2009, 2010; Ivanenko et al., 2012; Landers et al., 2014; Menzel et al., 2011; Packmor et al., 2015; Packmor and

Riedl, 2016; Plum et al., 2015; Plum and George, 2009; Pointner, 2015, 2017; Pointner et al., 2013, see also review of Vincx et al., 1994 and citations therein).

Therefore, we aimed to identify the potential influence of geological formations on the abundance and composition of Harpacticoida. For this purpose, we targeted adult harpacticoid Copepoda collected from both sides of the MAR along the VFZ and from the Puerto Rico trench.

Specifically, we aimed to address the following questions:

Does the composition of Harpacticoida change along 1.) the VFZ (longitudinal East-West transect) and the Puerto Rico trench (depth gradient) at different taxonomic levels?

Does the abundance of the Harpacticoida families differ along 2.) the VFZ (longitudinal East-West transect) and the Puerto Rico trench (depth gradient)?

In order to address these questions, we examined collected specimens at family level. Additionally, selected families (Argestidae Por, 1986; Cletodidae T. Scott, 1905, Zosimeidae Seifried, 2003, and Canthocamptidae Brady, 1880) were examined at genus and species level. We also tested for associations between differences in the community structure and abundance between regions with food variables, grain size and water depth.

2. Material and methods

2.1. Study area and sampling

During the Vema Transit Expedition (SO237) on board of RV *Sonne*, nine stations were sampled with a multiple corer (MUC) between the 14th of December 2014 and the 26th of January 2015 along the VFZ and Puerto Rico trench located in the North Atlantic. Eight out of nine stations were used for analyses of Harpacticoida. Five stations were located in the VFZ; with A1 and A3 situated on the Eastern side of the MAR (East Vema), A4 in a transform fault (Central Vema), and B1 and B2 on the Western side of the MAR (West Vema). Three stations were located in the Puerto Rico trench: two at the trench floor (hadal; C1 and C2), and one in the upper slope of the trench (C3) (for more details see Table 1; Fig. 1a, b).

At each station, three MUC-hauls were deployed (exception B1: only 2 successful hauls). From each haul, two cores were used for

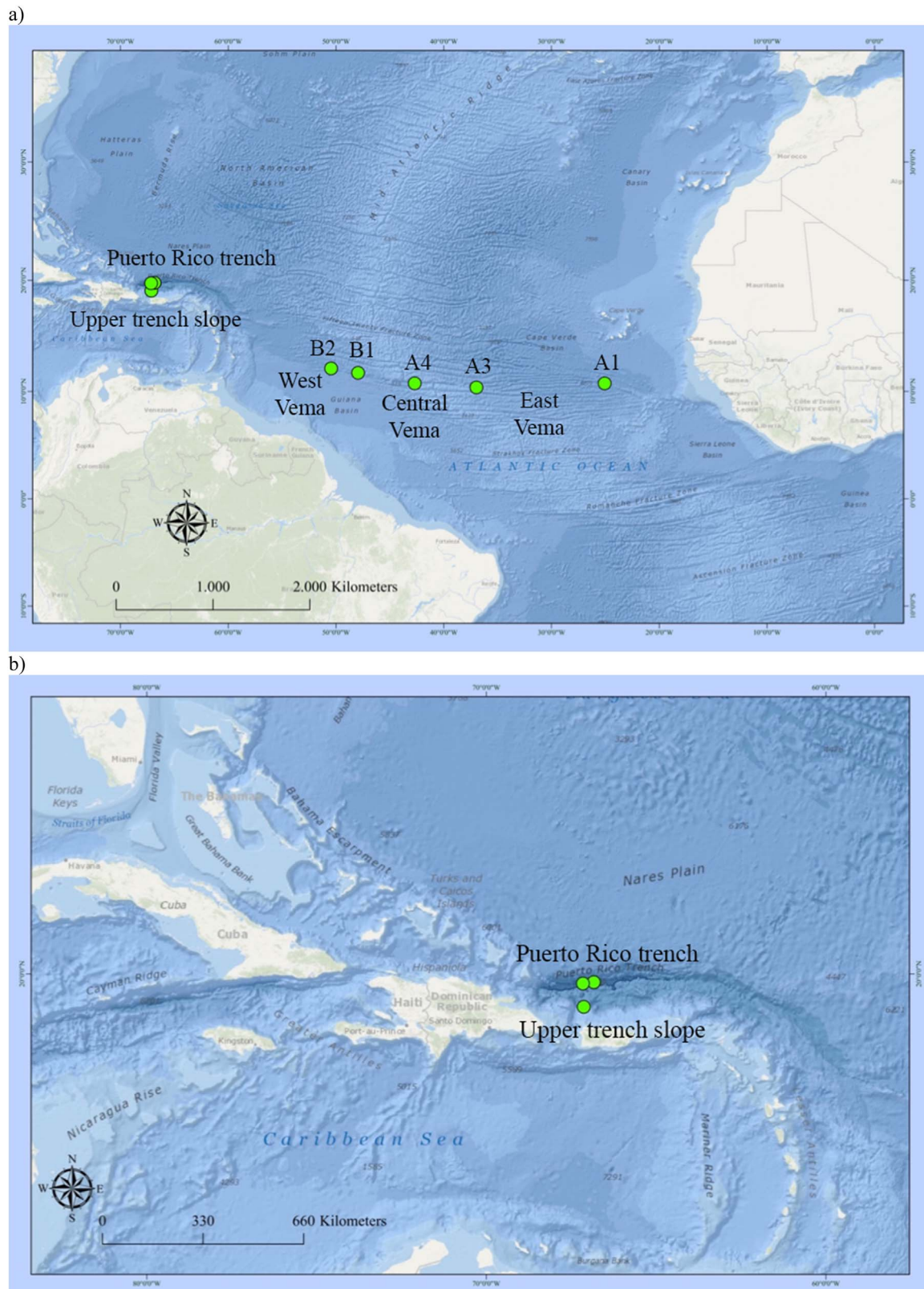


Fig. 1. Study area of the transatlantic expedition SO237. A) Overview map and b) detail map of the Puerto Rico trench. Source Basemap: ESRI, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and others.

community analyses of harpacticoid Copepoda. For this purpose, the top 5 cm layer of the sediment cores was extracted and fixed with either a buffered formaldehyde solution (4%) or DESS (dimethyl sulfoxide with EDTA and NaCl). DESS has the advantage that animals can be

studied morphologically as well as genetically (Yoder et al., 2006). An additional core (frozen at $-20\text{ }^{\circ}\text{C}$) was taken for the investigation of sediment environmental variables.

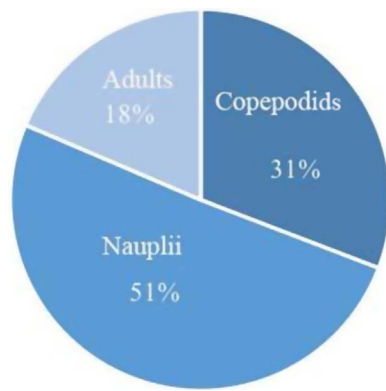


Fig. 2. Composition of Copepoda life history stages from the transatlantic expedition SO237 in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic (n = 4899).

2.2. Sample processing

2.2.1. Harpacticoida

In the laboratory, sediment was sieved (32 μm) and centrifuged following McIntyre and Warwick (1984). After centrifugation, samples were refixed with either a buffered formaldehyde solution (4%) or DESS and stained with bengal rose. All Harpacticoida were sorted and counted under a stereo microscope (Leica MZ 12.5) and separated in different life-history stages (adults, copepodids, nauplii), as well as gender of selected families (male, female). Taxonomic identification of adult Harpacticoida was based on Huys et al. (1996), Lang (1948) and Wells (2007). Zosimeidae were assigned according to Seifried (2003), Parameiropsidae according to Corgosinho and Arbizu (2010) and Rometidae according to Seifried and Schminke (2003). The families Argestidae, Cletodidae and Zosimeidae as well as one genus of the Canthocamptidae (*Metahuntmannia* Smirnov, 1946) were determined down to working species level. We chose these families as they were easy to detect in the samples due to their large body size of up to approximately 1 mm length, as well as their high diversity and wide distribution (e.g. Dahms and Pottek, 1992; George, 2004; Menzel and George, 2012; Koller and George, 2011; Menzel et al., 2011; Schriever, 1983, 1984).

2.2.2. Environmental variables

Grain-size distribution was determined with a Malvern Mastersizer 2000 (0.02–2000 μm size range). Sediment samples for total organic carbon (%TOC) and nitrogen content (%TN) were freeze-dried, homogenized, and acidified with 1% hydrochloric acid. Contents were then determined using the Flash EA 1112+ Mas 200 Elemental Analyser. Total organic matter content (%TOM) was determined by weighing after combustion at 550 $^{\circ}\text{C}$.

2.3. Data analyses

A Kruskal-Wallis test was used to test for differences in the total abundance of adult Harpacticoida within regions. To assess community similarity and species diversity, raw data of abundances was summarized in taxa-haul matrices for each taxonomic level. Similarities between regions (classified in East Vema, West Vema, Central Vema, Puerto Rico trench and upper trench slope) were calculated with the Cosine coefficient and non-metric multi-dimensional scaling (nMDS, Kruskal, 1964). Ordinations were used to illustrate spatial patterns of community structure. The Cosine-similarity is a qualitative measure for the similarity of communities, which illustrates the structural characteristic clearer than quantitative measures. Two objects are compared by their common dimensions and absences are not considered (Pfeifer et al., 1998). PERMANOVA was performed to test for significant differences between the regions and PERMDISP was conducted to test for

dispersion between the tested groups (Anderson, 2001; Anderson et al., 2006). We used the similarity percentages breakdown (SIMPER) procedure (Clarke, 1993) to calculate the mean percent contribution of variables to the dissimilarity between objects. SIMPER thus identifies the major contributor-variables of differences between groups detected by methods such as PERMANOVA. The Shannon ($H \log_e$) and the Simpson index (1-D) were chosen as biodiversity indices. Equitability (J' or Pielou evenness) was calculated to examine how evenly the individuals are distributed among the species. Species numbers were compared with ANOVA and Scheffe post-hoc test (normality assumption satisfied, tested by Shapiro-Wilk test). To test for relationships between Harpacticoida and environmental variables (total content of organic carbon (%TOC), total content of organic matter (%TOM), total content of nitrogen (%TN), grain size (D 4.3 volume weighted mean), and water depth (m)), a Canonical Correspondence Analysis (CCA) was carried out (Ter Braak, 1986). The principle of a CCA is to perform multiple regressions between dependent (taxa and sites) and independent variables (environmental factors) (Leyer and Wesche, 2007). Eigenvalues of the CCA axes show in which extent the taxa- or site-(region) values are separated along the axes (Leyer and Wesche, 2007).

The software PAST (version 3.1) was used for conducting the nMDS plot, PERMANOVA and SIMPER, diversity indices and CCA. Boxplots, Shapiro-Wilk test, ANOVA and the Kruskal-Wallis ANOVA were visualized and calculated using the software Statistica (version 10). PERMDISP was performed using the software R version 3.4.3. (R Development Core Team 2016) with the vegan (Oksanen et al., 2016) and LSA (Wild, 2015) packages. We used the ArcGIS software version 10 (Esri) to display the study area.

3. Results

3.1. Abundance, composition and biodiversity of Harpacticoida in the VFZ and Puerto Rico trench

A total of 4899 Copepoda were collected during this sampling campaign. Among the different life history stages, nauplii were found to dominate (51%), followed by copepodids (31%). Adult Copepoda comprised the smallest proportion (18%) of the total community (see Fig. 2). This distinct pattern of copepod life history stages was consistent across all regions.

For the following analyses, 837 adult animals were used. Highest total abundances of Harpacticoida were found in East Vema (Fig. 3). Comparing total abundance of Harpacticoida between regions, the

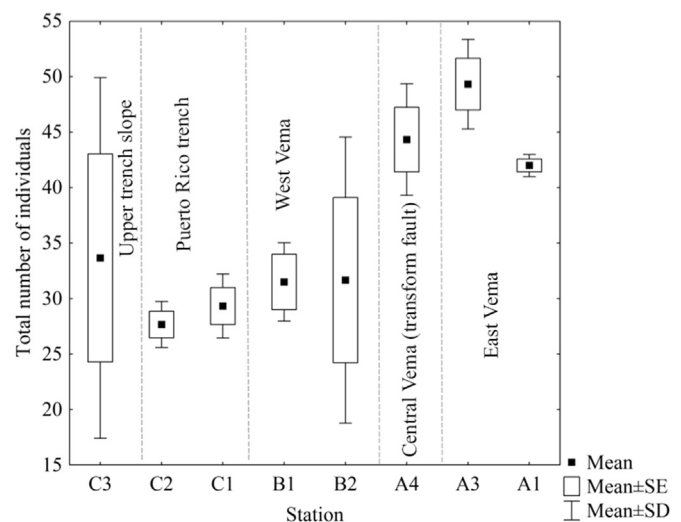


Fig. 3. Total abundance of adult Harpacticoida per station from the transatlantic expedition SO237 in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic. (n = 837).

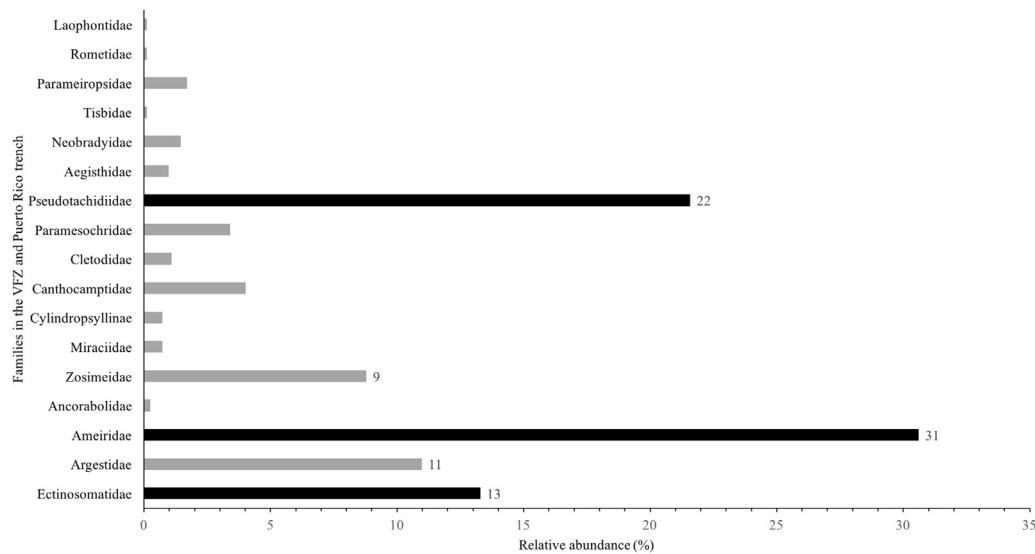


Fig. 4. Relative abundance (%) of all families across all regions based on the classification of adult harpacticoids ($n = 837$) from the transatlantic expedition SO237 in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic.

Kruskal-Wallis test showed significant differences between East Vema and West Vema ($p = 0.005$), as well as between the Puerto Rico trench and East Vema ($p = 0.001$). No significant differences were found between the Puerto Rico trench floor and upper trench slope of the Puerto Rico trench.

Identification of adult Harpacticoida resulted in 16 families and 1 subfamily: Ameiridae Boeck, 1865, Aegisthidae Giesbrecht, 1893, Ancorabolidae Sars 1909, Argestidae, Canthocamptidae, Cyliropsyllinae Sars 1909, Cletodidae, 1904, Ectinosomatidae Sars, 1903, Miraciidae Dana, 1846, Neobryidae Olofson, 1917, Paramesochridae, Parameiropsidae, Pseudotachidiidae Lang, 1936, and Zosimeidae, as well as Tisbidae Stebbing, 1910, Rometidae and Laophontidae T. Scott, 1905.

Across all regions, five harpacticoid families were most abundant: Ameiridae (31%), Pseudotachidiidae (22%), and Ectinosomatidae (13%), followed by Argestidae (11%) and Zosimeidae (9%, Fig. 4). However, in the trench floor Pseudotachidiidae were more abundant than Ameiridae. Furthermore, higher relative abundances of Zosimeidae and Paramesochridae occurred in the trench. In the upper trench slope region, Neobryidae were found among the most common families (Fig. 5).

As mentioned above, for further analysis on genus and species level Argestidae, Canthocamptidae, Cletodidae and Zosimeidae were selected. Across the entire study area, these four families consisted of the following 11 genera: *Pseudozosime* T. Scott, 1912, *Zosime* Boeck, 1873, *Metahuntemannia*, *Cletodes* Brady, 1872, *Stylicletodes* Lang, 1936, *Argestidae* gen. 1, *Malacopsyllus* Sars, 1911, *Bodinia* George (2004), *Argestes* Sars, 1910, *Mesocletodes*, and *Eurycletodes* Sars (1909). In general, the most abundant genera were *Zosime* ($n = 64$ individuals) and *Mesocletodes* ($n = 42$ individuals). In the Puerto Rico trench and Central Vema (transform fault) most individuals also belonged to *Zosime*, whereas *Mesocletodes* was found to be dominant in the upper trench slope and East Vema. In West Vema, *Zosime*, *Eurycletodes* and *Mesocletodes* showed the same dominance pattern in abundance. With regard to genus composition, out of the 4 analysed families, only 4 genera were present in the Puerto Rico trench floor, while 9 genera were present in the upper trench slope.

Eight genera were collected in Central Vema, 10 in East Vema and all 11 genera were present in West Vema (Table 2 and Fig. 6).

Furthermore, we investigated the gender ratio at genus level. The majority of Harpacticoida was female (62%, Fig. 7). Interestingly, 100% of all individuals of *Eurycletodes* were females. In contrast males

dominated (67%) within *Argestes* and *Malacopsyllus*.

Species were mostly found with low abundance, i.e. each species containing between 0 and 2 individuals over the entire dataset. A striking exception was *Zosime* sp. 8, which showed abundances between 0 and 8 individuals already in one core and its highest values in the Puerto Rico trench (C1 12-3). In total, 73 species within the selected families were recognized in this study. From these, 41 species were recorded only once (i.e., occurred as singletons) in our study area and seem to be endemic there (for example: *Eurycletodes* sp. 1 in Vema East, *Mesocletodes* sp. 7 in the Puerto Rico trench). Since we used working species, no generalizations for other study sites can be made. The highest number of species was found in haul A3 6-3 (Vema East, $n = 13$ species). Across the entire data set, *Mesocletodes* was most speciose, while *Zosime* exhibited the highest overall abundance. Based on the regional diversity in our study area, the highest overall species number was found in Vema East and at the upper trench slope. The trench floor on the other hand was characterized by a low number of species, but high abundances of individual species. By comparing the species numbers between our individual regions, the ANOVA showed significant differences ($p < 0.01$). The Scheffe post-hoc test revealed significant differences only between East Vema and the Puerto Rico trench floor ($p < 0.01$). No significant differences between East and West Vema or the Puerto Rico trench and its upper slope were found. An overview of the alpha biodiversity is presented in Table 3 while Table 4 shows the number of species as well as the corresponding total number of individuals and the relative contribution of individuals (%) of the entire study area. In Table 3, clearly all indices are lower in the trench compared to our other investigated regions in our study area.

3.2. Community analyses of Harpacticoida in the VFZ and Puerto Rico trench

Similarity analyses on family level, (nMDS plot, see Fig. 8) show a separation of harpacticoid communities in the Puerto Rico trench floor from those in the VFZ and in the upper trench slope of the Puerto Rico trench. Additionally, the data from East and West Vema show a distinction. However, the communities within all regions show high variation. On genus level, no clear distinction between the studied regions is visible due to high variance in the dataset (Fig. 9) while again all studied regions are more distinct from each other on species level (Fig. 10).

PERMANOVA revealed significant differences between the

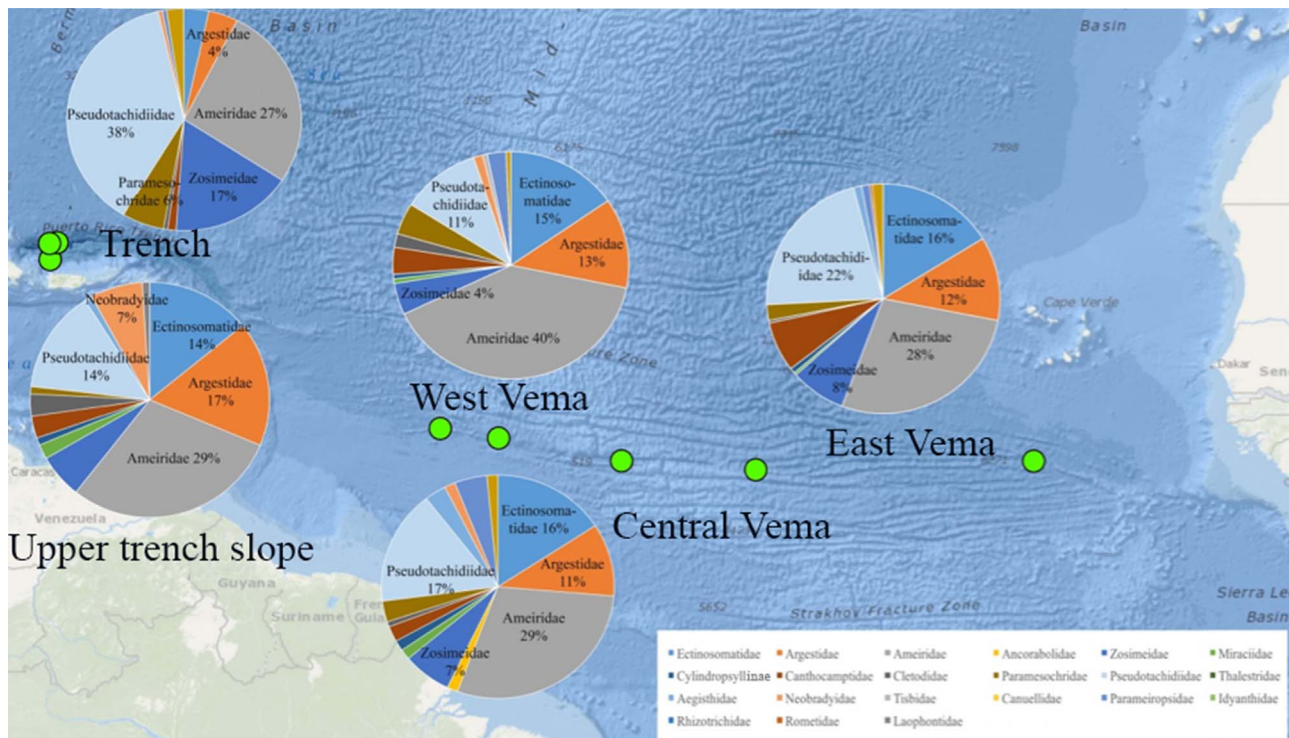


Fig. 5. Overview of the relative abundance (%) and composition of harpacticoid families for each region in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic (East n = 274, Central n = 133, West n = 158, upper trench slope n = 101, trench n = 171).

communities in the trench floor and upper trench slope and between the Puerto Rico trench and East Vema on all taxonomic levels (see summary of full PERMANOVA results in Table 5). Further significant differences were found between East and West Vema for family and species composition. SIMPER analysis revealed that Pseudotachidiidae, Ameiridae and Ectinosomatidae contributed mostly to the overall dissimilarities between the regions, followed by Argostidae and Zosimeidae (Table 6) on family level. *Zosime* and *Mesocletodes* had contributed the most to the dissimilarity on genera level. The dissimilarities between the Puerto Rico trench and its upper slope on species level

were fully driven by *Zosime* sp. 2 (100% contribution).

However, PERMDISP showed several significant differences ($p < 0.05$) between some of the groups (see Table 5 for summary), thereby revealing dispersion effects (on family level: East Vema and Central Vema, Upper trench slope and West Vema, on genus level: East Vema and West Vema, Trench and West Vema, on species level: Central Vema and Trench, East Vema and Trench, Upper trench slope and Trench, West Vema and Trench).

Table 2

Abundance and composition of harpacticoid genera per haul (n = 2 added cores) in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic.

Haul	<i>Eury-cletodes</i>	<i>Meso-cletodes</i>	<i>Arges-tes</i>	<i>Bo-dinia</i>	<i>Malacop-syllus</i>	<i>Arges-tidae</i> gen.	<i>Styliclet-odes</i>	<i>Cleto-des</i>	<i>Meta-hunte-mannia</i>	<i>Zo-sime</i>	<i>Pseudo-zosime</i>
A1 2–3	1	5	1	0	0	0	0	0	4	2	0
A1 2–4	1	2	0	0	0	1	0	0	2	2	1
A1 2–5	0	1	0	0	0	0	0	0	0	4	2
A3 6–3	3	0	2	0	2	1	0	0	3	5	1
A3 6–4	0	4	0	0	0	0	0	0	1	2	1
A3 6–5	2	3	2	1	0	0	0	1	0	2	0
A4 8–2	1	1	1	0	1	0	0	1	0	4	0
A4 8–10	1	0	0	0	1	1	0	0	0	3	1
A4 8–11	1	2	2	0	1	0	0	0	0	0	1
B1 9–3	1	2	3	0	0	0	0	0	0	0	1
B1 9–4	2	1	0	0	0	1	0	0	0	1	0
B2 11–5	1	2	0	1	0	0	0	1	1	3	0
B2 11–6	2	1	0	0	2	0	1	0	2	1	2
B2 11–7	0	0	0	0	1	0	1	0	0	1	0
C1 12–3	0	3	0	0	0	0	0	0	0	8	0
C1 12–7	0	1	0	0	0	0	0	0	0	4	0
C1 12–8	0	1	0	0	0	0	0	0	0	6	0
C2 13–1	0	0	0	0	0	0	0	0	0	4	0
C2 13–2	0	1	0	0	0	0	0	1	0	1	0
C2 13–3	0	0	0	0	0	0	0	0	1	6	0
C3 14–3	1	2	0	0	1	0	0	0	0	0	0
C3 14–4	2	6	0	0	0	1	0	0	2	1	1
C3 14–5	0	4	0	0	0	0	1	1	0	4	2
Total	19	42	11	2	9	5	3	5	16	64	13

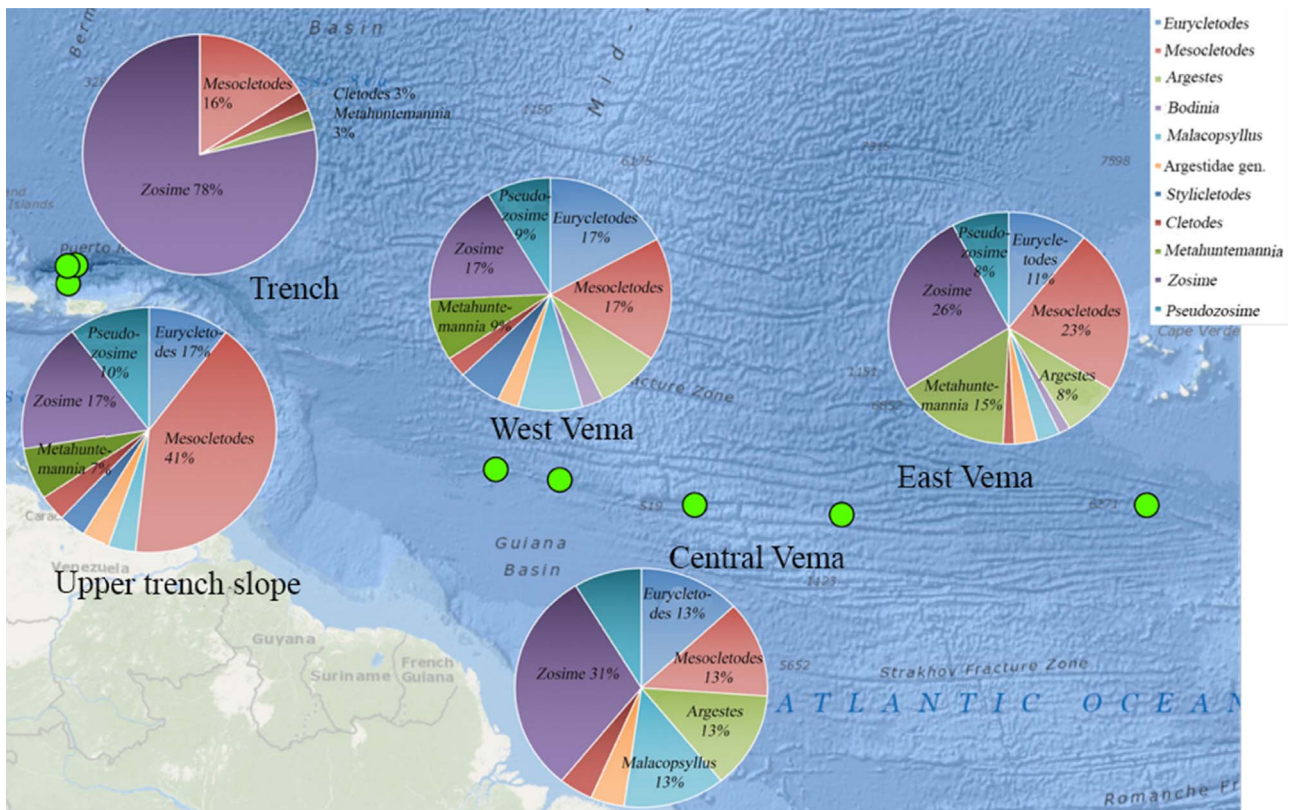


Fig. 6. Overview of the relative abundance (%) and composition of harpacticoid genera for each region in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic (Trench n=37, upper trench slope n=29, West n=35, East n=65, Central n=23, Selected genera are: *Zosime*, *Pseudozosime*, *Eurycletodes*, *Mesocletodes*, *Argestes*, *Malacopsyllus*, *Stylicletodes*, *Cletodes*, *Metahuntemannia*).

3.3. Canonical Correspondence Analysis (CCA) of Harpacticoida and environmental variables

An overview of the measured environmental variables can be found in Table 1. The CCA (Fig. 11a, b) displayed the environmental factors characterizing the stations and the harpacticoid community composition at family level. More than half (58.88%) of the total variance in the data set could be explained by axis 1, which is defined by TOM and TN (see Table 7 for a full summary of CCA eigenvalues). Fig. 11a) shows a clear relationship between trench stations and water depth characterized by environmental variables. At the upper trench slope and in West Vema, the grain size was increased. Fig. 11b) shows that most families (e.g. Ameiridae, Ectinosomatidae, Argestidae) were highly associated with grain size. Contrastingly, abundance and occurrence of Ameiridae seemed to depend on TOM. Most families were less influenced by TN. In contrast, the occurrence of the families Zosimeidae and Pseudotachidiidae depended more on TOC and water depth.

Fig. 12 shows the CCA of environmental variables and genus composition. Axes 1 (TOM) and 2 (all other environmental variables combined) explained 80.14% of the total variance. *Zosime* was highly

influenced by depth, TOC and TN. In contrast, *Mesocletodes*, *Pseudozosime* and *Metahuntemannia* mostly depended on the sediment grain size, whereas *Cletodes* showed a relationship with TOM. *Eurycletodes*, *Bodinia* and *Malacopsyllus* were influenced by TOM and grain size.

Fig. 13 shows the CCA of environmental factors and species. The first three axes combined explained 82.78% of the total variance. Axes 1 was defined by TOM and TN. Axes 2 was represented by depth, grain size and TOC. Fig. 13 shows that the species *Zosime* sp. 2, sp. 4, sp. 6 and *Zosime* sp. 8 were more abundant at deeper localities. For many species, the grain size was important (e.g. *Eurycletodes* sp. 4 and sp. 10, *Mesocletodes* sp. 24, *Zosime* sp. 1, *Cletodes* sp. 3, *Malacopsyllus* sp. 2, *Metahuntemannia* sp. 1 and sp. 3). *Bodinia* sp. 2 and *Mesocletodes* sp. 14 had a strong relationship with TOM, whereas e.g. *Mesocletodes* sp. 15 and *Pseudozosime* sp. 3 were depended on TOC. Many of the *Mesocletodes* species (e.g. *Mesocletodes* sp. 22, sp. 18, sp. 10, sp. 15, sp. 1) and *Zosime* sp. 7 were strongly influenced by TN.

4. Discussion

Here, we investigated the community composition and abundance

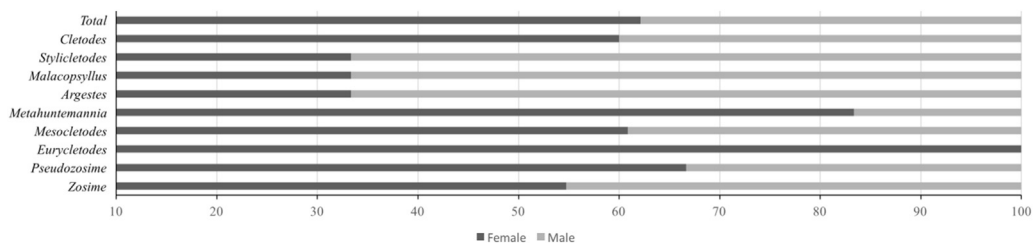


Fig. 7. Gender composition (relative abundance %) of the selected Harpacticoida genera in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic (n=132). Selected genera are: *Zosime*, *Pseudozosime*, *Eurycletodes*, *Mesocletodes*, *Argestes*, *Malacopsyllus*, *Stylicletodes*, *Cletodes*, *Metahuntemannia*.

Table 3
Alpha biodiversity of Harpacticoida (per haul) in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic: number of species, individuals, as well as biodiversity indices: Simpson (1-D), and Shannon (H (loge)′), and *equitability* (J′). n=2 added cores for each haul).

Region	Haul	Species number	Individuals	1-D	H (loge)′	J′
East	A1 2–3	9	13	0.86	2.10	0.95
	A1 2–4	7	9	0.84	1.89	0.97
	A1 2–5	6	8	0.78	1.67	0.93
	A3 6–3	13	16	0.91	2.51	0.98
	A3 6–4	9	9	0.89	2.20	1.00
Central	A3 6–5	10	11	0.89	2.27	0.99
	A4 8–10	6	7	0.82	1.75	0.98
	A4 8–11	5	6	0.78	1.56	0.97
	A4 8–2	8	9	0.86	2.04	0.98
	B1 9–3	7	7	0.86	1.95	1.00
West	B1 9–4	5	5	0.80	1.61	1.00
	B2 11–5	7	9	0.81	1.83	0.94
	B2 11–6	10	11	0.89	2.27	0.99
	B2 11–7	3	3	0.67	1.10	1.00
	C1 12–3	4	12	0.51	0.98	0.71
Puerto-Rico trench	C1 12–7	2	4	0.50	0.69	1.00
	C1 12–8	4	7	0.61	1.15	0.83
	C2 13–1	4	5	0.72	1.33	0.96
	C2 13–2	2	2	0.50	0.69	1.00
	C2 13–3	2	6	0.28	0.45	0.65
Puerto Rico upper trench slope	C3 14–3	2	2	0.50	0.69	1.00
	C3 14–4	12	17	0.89	2.36	0.95
	C3 14–5	6	10	0.80	1.70	0.95

Table 4
List of harpacticoid genera and associated species numbers, individual numbers and their relative contribution (%) in the Vema Fracture Zone and the Puerto Rico trench.

Species	No Species	Species (%)	No individuals	Individuals (%)
<i>Argestes</i>	4	5	11	6
<i>Argestidae</i> gen.	1	1	5	3
<i>Bodinia</i>	2	3	2	1
<i>Cletodes</i>	4	5	5	3
<i>Eurycletodes</i>	11	15	19	10
<i>Malacopsyllus</i>	5	7	9	5
<i>Mesocletodes</i>	26	36	41	22
<i>Metahuntemannia</i>	6	8	16	9
<i>Pseudozosime</i>	4	5	13	7
<i>Stylicletodes</i>	2	3	3	2
<i>Zosime</i>	8	11	64	34

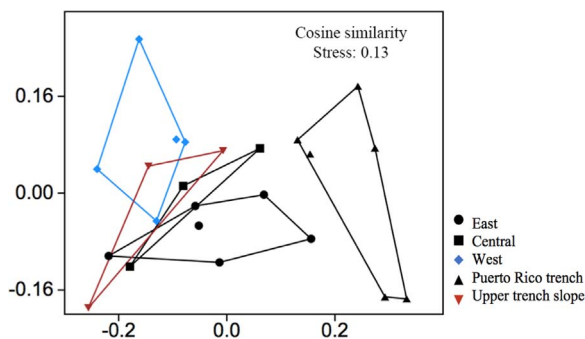


Fig. 8. nMDS-plot of the abundance data of harpacticoid families per region in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic based on Cosine similarity (stress: 0.13).

of Harpacticoida (Crustacea: Copepoda) along an East-West longitudinal transect (Vema Fracture Zone) and a depth transect (Puerto Rico trench) to identify environmental drivers of Harpacticoida distribution.

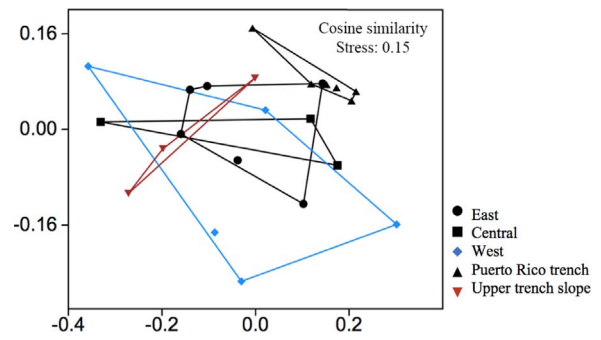


Fig. 9. nMDS-plots of the abundance data of selected harpacticoid genera per region in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic based on Cosine similarity (stress: 0.15).

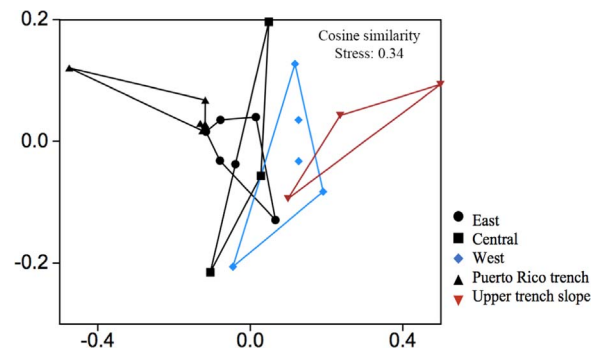


Fig. 10. nMDS-Plot of the abundance data of harpacticoid working species per region in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic based on Cosine similarity (stress: 0.34).

4.1. Life history stages and gender ratio of Harpacticoida

In our study, among all copepods, nauplii were most abundant (51%), while adults made up 18% of the total abundance. This relatively small abundance of adults is in line with the results reported by Mahatma (2009). Also, the dominance of nauplii among copepods in deep-sea sediments is corroborated by other studies from a variety of ecosystems (e.g., Büntzow, 2011 (seamount); Janssen, 2008 (marine cave); Mahatma, 2009 (Pacific deep sea)). Contrastingly, Ahnert and Schriever (2001) found that copepodids dominated the community in the deep sea in their study area in the Eastern Pacific. Previous studies showed that copepodids can make up to 50% of the general abundance in the deep sea (Shimanaga and Shirayama, 2003; Rose et al., 2005; Thistle et al., 2007; Shimanaga et al., 2008). However, the dominance of early life stages in our study possibly reflects the reproduction strategy (r-strategist) of harpacticoids and may also be due to small-scale aggregation after hatching (Dahms and Qian, 2004; Menzel and George, 2012). Moreover, for some Harpacticoida a delayed nauplii development was reported (Coull and Dudley, 1976), which means that they persist longer in a habitat without adults to utilize different resources and thus avoid direct competition (Dahms and Qian, 2004). Nevertheless, the proportion of the different life-history stages in general fluctuates and is depended on environmental changes, such as food supply, predation pressure or competition (Hicks and Coull, 1983).

The gender ratio in this study was strongly biased towards females. This finding is in line with previous studies on Harpacticoida in general (Shimanaga and Shirayama, 2003; Shimanaga et al., 2009; Thistle and Eckman, 1990). The most likely reason for female-biased sex ratio is that harpacticoid males mature earlier and live shorter after their adult molt in comparison to females. It was already observed in shallow waters that adult harpacticoid males die after successful mating (Hicks and Coull, 1983). While for some Harpacticoida it has been suggested that they lack clear dimorphic structures (Coull, 1973), in most deep-

Table 5

Results of the PERMANOVA and PERMDISP at family, genus and species level based on Cosine similarity from the Vema-TRANSIT expedition in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic. Abbreviations and tested region groups: UTS=upper trench slope of the Puerto Rico trench, Trench=Puerto Rico trench floor, East=East Vema Basin, West=West Vema Basin, Central=Central Vema Basin (transform fault). Significant results ($p < 0.05$) are marked with*.

Group of regions	VFZ families	VFZ genera	VFZ working species	Group of regions	Puerto Rico trench families	Puerto Rico trench genera	Puerto Rico trench working species
PERMANOVA	p, F	p, F	p, F	PERMANOVA	p, F	p, F	p, F
East-West	0.01*, 3.45	0.67, 0.60	0.041*, 2.05	Trench-UTS	0.013*, 3.67	0.01*, 22.73	0.01*, 4.6
Central-West	0.29, 1.28	0.96, -0.03	0.72, 0.65	Trench-West	0.001*, 7.62	0.01*, 5.5	0.01*, 5.86
Central-East	0.73, 0.58	0.45, 0.83	0.28, 1.24	UTS-West	0.57, 0.71	0.52, 0.84	0.29, 1.14
PERMDISP	p	p	p	PERMDISP	p	p	p
East-West	0.47	0.03*	0.42	Trench-UTS	0.06	0.25	0.01*
Central-West	0.08	0.36	0.16	Trench-West	0.52	0.01*	0.01*
Central-East	0.02*	0.35	0.08	UTS-West	0.05*	0.15	0.24

Table 6

SIMPER results based on Cosine similarity from the Vema Fracture Zone and the Puerto Rico trench, North Atlantic. The five main contributors of the harpacticoids on family, genus and species level to dissimilarities are shown.

Fami-lies	East – West contrib. %	West – Trench contrib. %	Trench – US contrib. %	Gen- era	West – Trench contrib. %	Trench – US contrib. %	Spec- ies	East – West contrib. %	West – Trench contrib. %	Trench – US contrib. %
Ameiridae, 61.06		Amei-ridae, 63.1	Amei-ridae, 48.88		Meso-cletodes, 20.03	Zosime, 57.03		Zosime sp. 1, 47.53	Meso-cletodes sp. 6, 100	Zosime sp. 2, 100
Ectino-somatidae, 14.28		Pseudo-tachidi-idea, 23.71	Pseudo-tachidi-idea, 35.2		Zosime, 18.84	Meso-cletodes, 41.11		Meta-hunte-mannia sp. 1, 14.81		
Pseudo-tachidi-idae, 12.78		Zosime-idea, 5.06	Zosime-idea, 6.46		Metahunte-mannia, 15.61	Cletodes, 1.23		Pseudo-zosime sp. 1, 10.4		
Argestidae, 8.26		Ectino-somatidae, 3.12	Arges-tidae, 4.96		Malacopsyl-lus, 10.47	Meta-hunte-mannia, 0.63		Argestes sp. 1, 6.05		
Zosime-idae, 2.08		Arges-tidae, 3.05	Ectino-somati-dae, 3.65		Argestes, 9.99			Meso-cletodes sp. 4, 3.97		

sea species sexual dimorphism is highly apparent (George, 2004, 2008; Hicks and Marshall, 1985; Menzel, 2011; Willen, 2005). Additionally, environmental variables have been suggested, to influence sex determination in Copepoda. Gender determination is e.g. affected by temperature (Katona, 1970), food quantity and quality (Irigoiien et al., 2000; Mauchline, 1998), population density (Heinle, 1969) and hydrostatic pressure (Vacquier and Belsler, 1965). Further, intersexuality is known from Copepoda and even morphological intersexuality in harpacticoids has been reported (Moore and Stevenson, 1994). However, its control mechanisms and impact on the population are poorly understood (reviewed by Gusmão and McKinnon, 2009).

4.2. Abundance, biodiversity, composition and community structure in relation to the environmental variables

4.2.1. Vema Fracture Zone

In the VFZ, the highest abundances of Harpacticoida were recorded in East Vema, and a decrease in abundance from East to West was apparent and also confirmed by the Kruskal Wallis test, which showed significant differences between the total Harpacticoida abundance in East and West Vema. Previously, an East-West gradient in meiofauna abundance has been found in other studies and this was attributed to stronger bottom currents in the Western North Atlantic (Richardson et al., 1981; Schmidt (xx), (this issue), Vincx et al., 1994). This pattern is supported by the increase in sediment grain size from East to West found in our study, as fine sediment would not be deposited in an area with strong currents. In addition, higher abundances in the Eastern Atlantic basin compared to the Western basin were related to higher surface primary production in the Eastern basin (Schmidt (xx), (this issue), Lins et al., 2016, (this issue), Thiel, 1983). In fact, our results are in accordance with this higher surface primary production in the Eastern basin, as the abundance of many taxa was strongly influenced by the availability of food, as shown by the CCA (TOM, TOC and TN). The importance and controlling function of food supply for meiofauna

has also been confirmed by previous studies (Baguley et al., 2006; Schewe and Soltwedel, 2003; Shirayama, 1984; Vincx, 1994). Another reason for different harpacticoid abundances found in East and West Vema in this study might be the presence of hard bottom which occurred in the Western basin (nodules and manganese crust, Devey et al., (xx), (in this issue)). As we sampled with a gear (MUC) which is usually used for soft bottom, it cannot be excluded that lower abundances of meiofauna as found in the Western basin were caused by insufficient sampling.

In addition to differences in abundance, PERMANOVA results revealed significant differences in the community composition between East and West Vema on family and species level while no differences were found on genus level. However, PERMDISP revealed significant differences within the East and West Vema groups on genus level, which indicates high dispersion within these groups on genus level.

In general, many studies revealed a similar taxonomic composition at family level as found in our study and already stated a cosmopolitan distribution of harpacticoid families (George et al., 2014; Gheerardyn and Veit-Köhler, 2009; Menzel, 2011; Menzel et al., 2011; Vincx et al., 1994). Ameiridae, for example, is generally a widespread and abundant family (e.g. George, 2005: Magellan region; Kitahashi et al., 2012: Kuril Kamchatka trench; Rose et al., 2005: Angola basin) and were also dominant in most regions of our study area (with exception of the trench) contributing most to dissimilarities between sampling sites. Also, some genera which were found to be most abundant throughout our study region, e.g. *Mesocletodes* and *Zosime* might be cosmopolitans. In fact, these well-known members of the Harpacticoida exhibit an overall large geographic range (George, 2005; Koller and George, 2011). The most abundant taxa occurring in the study area are likely to be better adapted to the prevailing conditions, and may be reproducing faster or more efficiently (production of more eggs or reproduction only at good environmental conditions) than less successful species. In this context, a delayed development of eggs and a survival stage (dormancy) is known from calanoid copepods in an adverse environment (Ranade,

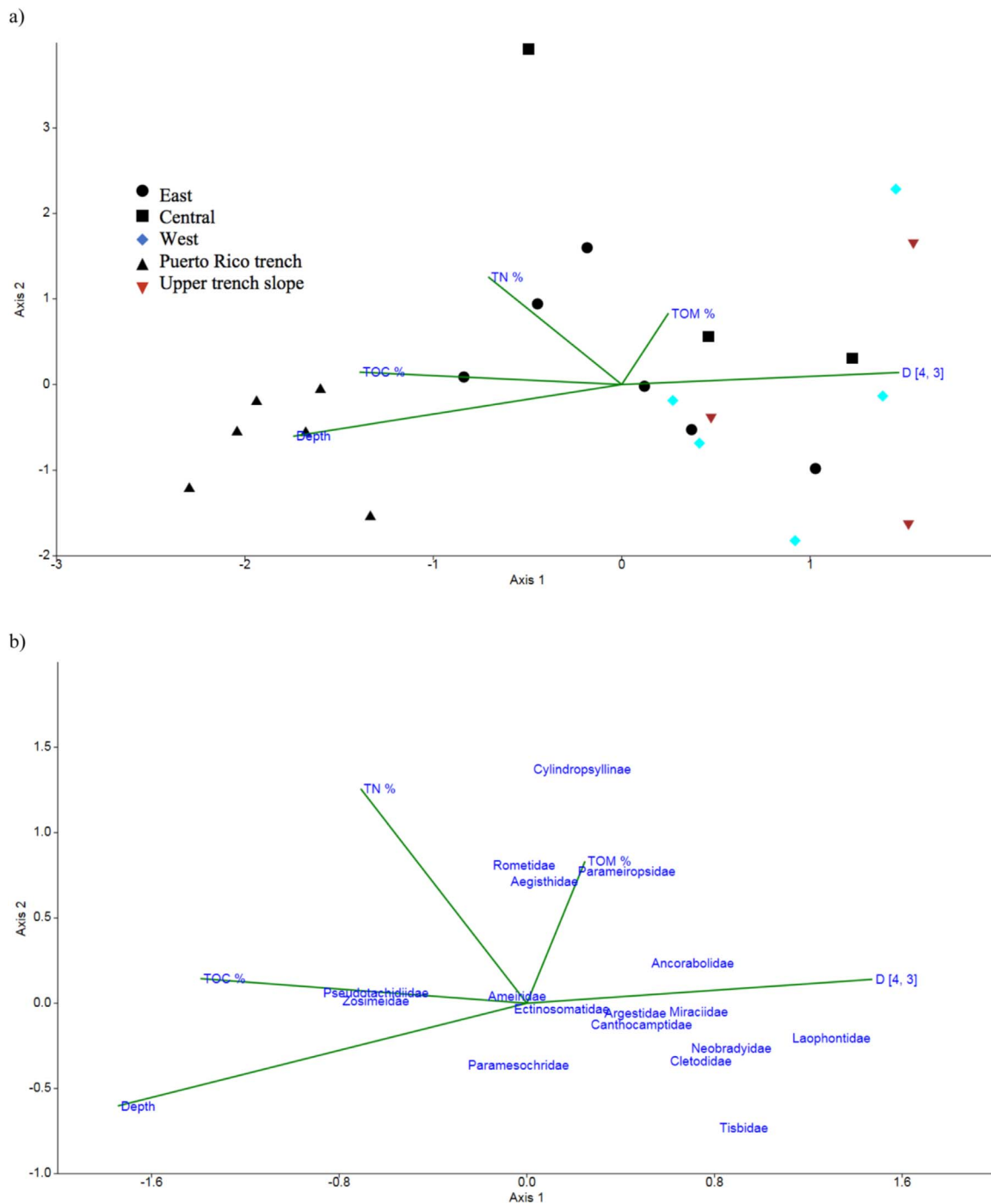


Fig. 11. Canonical correspondence analysis of the abundance data and environmental variables in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic; analyses with sites (a), and with harpacticoid families (b).

Table 7

Eigenvalues of all CCA axes at harpacticoid family, genus and species level from the Vema-TRANSIT expedition in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic.

Axis Families	Eigenvalue	%	Axis Genera	Eigenvalue	%	Axis Species	Eigenvalue	%
1	0.12	58.9	1	0.24	53.15	1	0.72	33.64
2	0.04	18.8	2	0.12	26.99	2	0.60	28.21
3	0.03	13.6	3	0.06	13.61	3	0.45	20.93
4	0.02	8.72	4	0.03	6.241	4	0.37	17.22
5	1 E-06	0.0005	5	4 E-06	0.0009	5	5.63	0.003

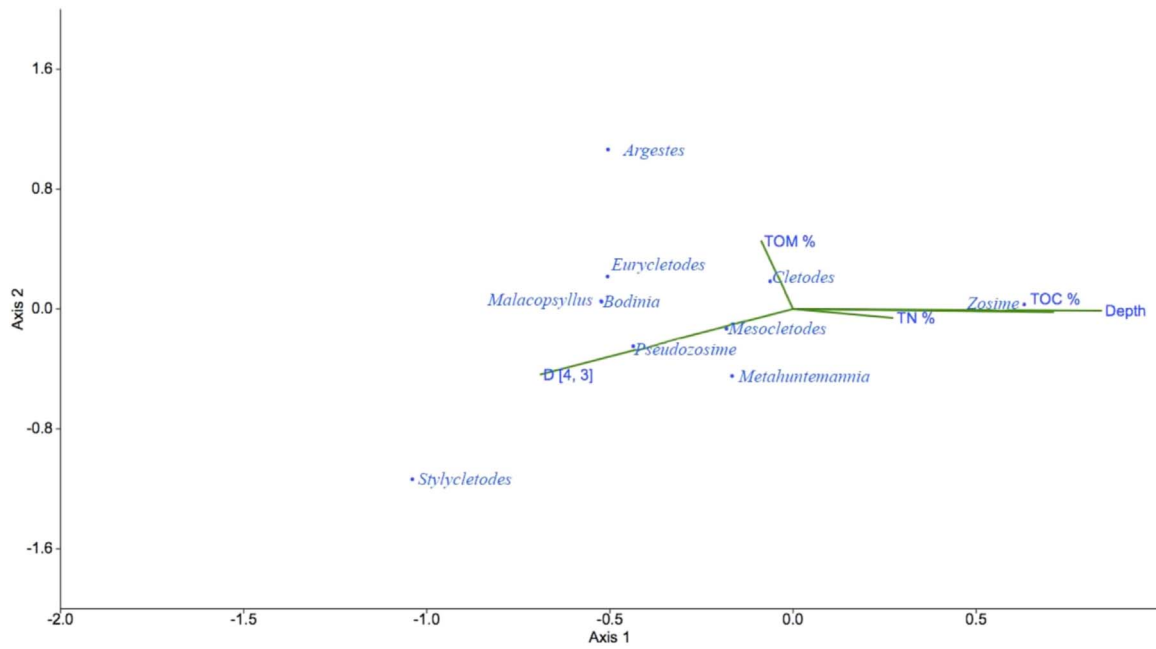


Fig. 12. Canonical correspondence analysis of selected harpacticoid genera and environmental variables in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic.

1957; Williams-Howze, 1997).

In the entire study area, 73 species were identified. In comparison, George et al. (2014) reported 132 species within the selected families in the Angola Basin (Northeast Atlantic, depth range: 5389–5448 m). Using identical core numbers (n=68) as means of comparing our results with this study showed approximately 120 species for George et al. (2014). However, George et al. (2014) found the highest harpacticoid species number ever recorded for a single deep-sea locality and attributed this to increased food supply there. In general, the total species number recorded in a sampling campaign may also be considerably affected by features specific to a sampling region, specifically habitat heterogeneity, environmental stability, water productivity, resource content, combination of multiple colonization and radiation events, or

‘age’ of a region, which affects colonization time (geologically older oceans or regions usually host more species than young ones) (Stoch, 1995).

As shown by ANOVA, no significant differences between the species numbers in West and East Vema occurred. In support of our results, Guggolz et al. (2017, this issue) recently investigated polychaetes in the VFZ without finding significant differences in the diversity, they however reported a tendency of slightly lower values for West Vema. In our study, we already found very variable species numbers in the different hauls of the respective regions. Thus, tendencies of slightly lower values for West Vema could not be shown but might explain why we found no significant differences between East and West Vema. Patchiness in harpacticoid species on small scales has

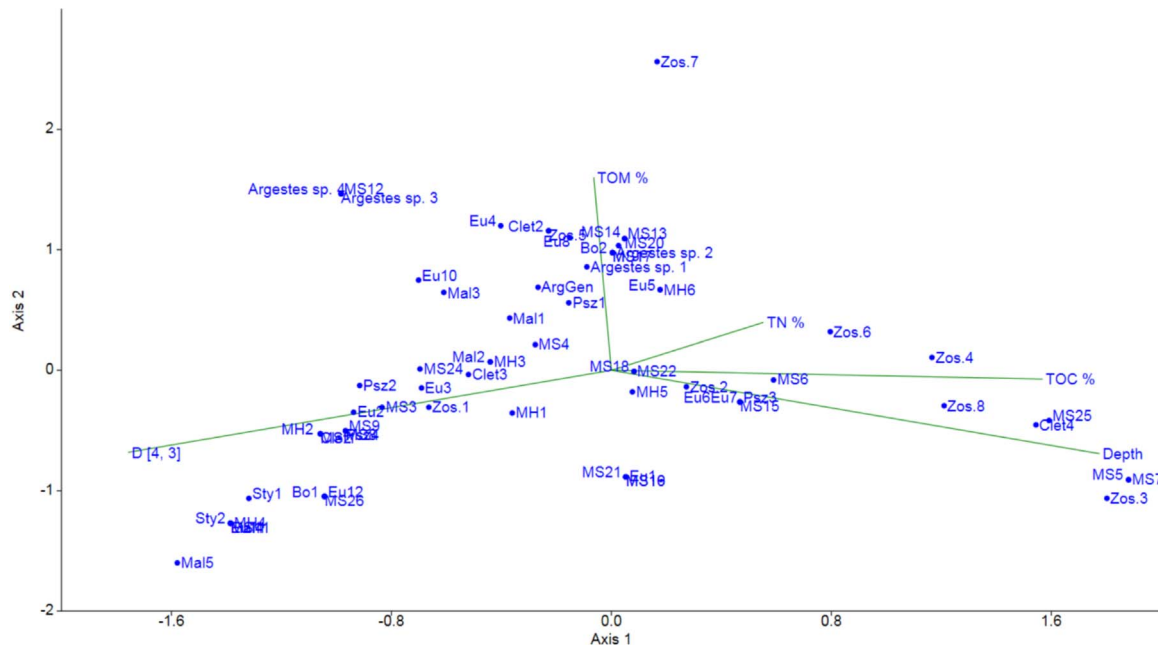


Fig. 13. Canonical correspondence analysis of harpacticoid species and environmental variables in the Vema Fracture Zone and the Puerto Rico trench, North Atlantic. Abbreviations of species names: Eu = Eurycletodes, MS = Mesocletodes, Zos = Zosime, Psz = Pseudozosime, Mal = Malacopsyllus, MH = Metahuntemannia, Clet = Cletodes, Sty = Stylicletodes, Bo = Bodinia, ArgGen = Argestidae genera.

already been documented by other studies (Rose et al., 2005; Thistle, 1978). An explanation for the patchiness in (meio)faunal small-scale distribution might be biogenic structures such as burrows, depressions and hills which are produced by macrobenthos as well as patchy food input (Grassle, 1989; Thistle & Eckman, 1988).

The equitability (J') of Harpacticoida found in the present study (~ 1) suggests a very even distribution of individuals among species due to the presence of many rare taxa. Indeed, when considering harpacticoid species numbers per core, most species were represented by only 1 individual (singletons). This result is not surprising, but rather typical for deep-sea harpacticoid communities (Rose et al., 2005). The singletons found in our study seemed to be endemic in their respective region; e.g. in the VFZ. Nevertheless, no generalizations can be made as we dealt with working species, so their distributional range outside the VFZ and Puerto Rico trench remains unknown.

4.2.2. Puerto Rico trench

The Puerto Rico trench showed significantly lower abundances than its upper slope at all taxonomic levels examined. However, on species level, high dispersion was shown by the PERMDISP analysis. Thus, differences on species level found by PERMANOVA accounted for a high amount of dispersion. Other studies previously recorded differences in the community structure between abyssal, trench slope and hadal environments (Fujii et al., 2013; Gallo et al., 2016; Jamieson et al., 2011; Kitahashi et al., 2013). Alongside our findings, this supports the theory of the existence of an ecotone between abyssal and hadal. An ecotone is a transition zone between two defined habitats showing an abrupt change in taxa composition (Jamieson et al., 2011).

The harpacticoid communities in the Puerto Rico trench were dominated by Pseudotachidiidae, and contained a high proportion of Zosimeidae, while the VFZ and upper trench slope were dominated by Ameiridae. Ectinosomatidae were less abundant in the Puerto Rico trench but very abundant in the VFZ. Pseudotachidiidae and Zosimeidae seem to adapt easier on the highly dynamic environment in the trench. Disturbances, such as turbidities, frequently occur in the Puerto Rico trench (Richardson et al., 1995) and result in a perturbation of the seabed and inhabiting fauna by mixing of the sediment (Leduc and Pilditch, 2013; Moodley et al., 2000). Hence, the high abundance of the families Pseudotachidiidae and Zosimeidae in the Puerto Rico trench might not only be due to their high adaptability, but also to their possible preference for smaller grain size and higher sediment TOC content, as displayed in the CCA. As already mentioned above, grain size and food availability generally are known to be important for the distribution of meiofauna (Danovaro et al., 2002; Dashtgard et al., 2008; Etter and Grassle, 1992; Gambi and Danovaro, 2016; Kitahashi et al., 2012; Leduc et al., 2016; Levin et al., 2001; Montagna, 1982; Shirayama, 1984). Thus, the environmental ambient conditions at the trench floor likely drive this distinct community composition. Among investigated families, *Zosime* represented the most dominant genus with a relative abundance of 78% in the Puerto Rico trench floor. No other harpacticoid genus was present at comparatively high abundances in our study. Generally, the genus *Zosime* is widely distributed (Koller and George, 2011), which can probably be linked to its high capacity in adapting to changing environmental conditions.

As shown by ANOVA, the Puerto Rico trench floor differed not only in terms of composition from other stations but also in total species number, which was much lower than the number found in the VFZ. The lower species number and the dominance of *Zosime* in the trench is most likely shaped by the frequent disturbances there (Jamieson et al., 2010). Thistle (1981, p. 223) already pointed out that “some species become abundant early in the recolonization of a disturbed patch, reflecting their dependence on disturbed localities for their persistence in the local community.” Moreover, in a model of Grassle and Sanders (1973), opportunistic species colonize disturbed patches early due to their rapid dispersal and high reproductive rates. Re-colonization after disturbances can proceed very slowly and thus be characterized by a

variety of species (Cuvelier et al., 2014; Giere, 2009; Gollner et al., 2015). Furthermore, the sampled depth of > 8000 m in the Puerto Rico trench can be considered as an isolating factor, similar to an island, and contribute to or even constitute species poverty (see theory of island biogeography, Wilson and MacArthur, 1967). In fact, our results showed a strong relationship between the dominating taxa in the Puerto Rico trench and depth (Zosimeidae and Pseudotachidiidae on family level, *Zosime* on genus level). However, on islands the rate of evolution (new species due to speciation) can be higher as the rate of species immigration which leads, in turn, to higher dependence on speciation than on immigration and extinction (Townsend et al., 2009). Species richness increases with increasing spatial heterogeneity, broader range of resources available and higher differentiation of species in their use of resources. This might explain our findings of higher abundances and species richness in the upper trench slope. The slope of the Puerto Rico trench is typically characterized by scarps and has apparently a continuing downward gradient (Ewing and Heezen, 1955). Together with the striking surface topography of the Puerto Rico trench slope these factors enhance the habitat heterogeneity and thus favor niche segregation (Jamieson et al., 2015; Guggolz et al., 2017 (in this issue); Kadmon and Allouche, 2007). The Puerto Rico trench may be characterized by fewer ecological niches (Connell and Orias, 1964) than the upper trench slope and East and West Vema.

5. Conclusion

In conclusion, our study revealed higher abundances of Harpacticoida in East Vema, in comparison to West Vema as well as differences in community composition. The East-West gradient was strongly driven by variations in food availability, primary production and current regime. The Puerto Rico trench, as an extreme habitat, had a lower total number of species, probably because only specialists or opportunists, who are adapted to frequent disturbances, may be able to live here. Due to isolation by depth, immigration of species is rather a slow process and species diversity is more likely to be directed by speciation as implied by the theory of island biogeography. The differences in taxa composition and taxa richness due to higher habitat heterogeneity in the upper trench slope and floor of the Puerto Rico trench support the existence of an ecotone.

Furthermore, the cosmopolitan nature of harpacticoid families and genera, as previously shown by other studies, could be substantiated. Finally, the detected sex-ratio towards females has also been reported by other studies but cannot yet be finally explained, while the dominance of early developmental stages most likely reflected the reproduction strategy (r-strategist) of harpacticoids.

With these results, our study contributes to the understanding of distribution, biodiversity and community structure of deep-sea meiofauna. Our results with regard to patterns of deep-sea (meio-)fauna in the Puerto Rico trench are especially valuable as trenches comprises one of the world's most extreme and poorly understood ecosystems due to its remoteness and difficult accessibility.

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