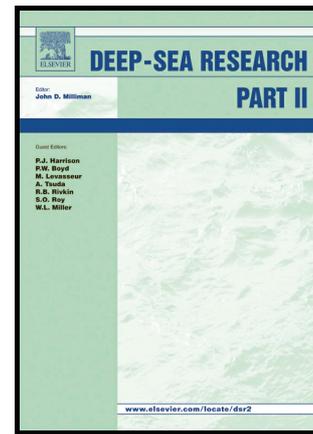


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Diversity of macrofaunal Mollusca of the abyssal Vema Fracture Zone and hadal Puerto Rico Trench, tropical North Atlantic

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Keywords: Atlantic, Bivalvia, Gastropoda, Scaphopoda, species richness

Abstract

While biodiversity patterns of Atlantic deep-sea bivalves and gastropods have served as model taxa for setting global latitudinal and bathymetric hypotheses, less is known on abyssal, amphi-Atlantic molluscan assemblage compositions. The Vema-TRANSIT expedition sampled 17 stations in the Vema Fracture Zone (VFZ) and the Puerto Rico Trench (PRT) by epibenthic sledge. These samples comprised a total of 1333 specimens and 64 morphospecies of the classes Caudofoveata (7 species), Solenogastres (7 spp.), Bivalvia (22 spp.), Gastropoda (24 spp.), and Scaphopoda (4 spp.) while Cephalopoda, Monoplacophora and Polyplacophora were absent. The majority of species was rare with 21 uniques (32.8% of all species) and 10 duplicates (15.6% of all species) and of these 15 (48% of rare/ 23.4% of all species) morphospecies were singletons and 8 (25.8% of rare/ 12.5% of all species) morphospecies were doubletons. Overall bivalves (686 specimens) were most abundant, followed by scaphopods (314 spec.), while solenogastres (180 spec.), caudofoveates (86 spec.) and gastropods (67 spec.) were less abundant. The abyssal macro-molluscan species composition did not vary significantly between the eastern and western Atlantic sides of the VFZ while abundances standardized to 1000 m² trawled area were higher on the eastern side. The abyssal PRT stations resembled the VFZ ones in species composition and abundances, in

the latter the eastern VFZ. The hadal PRT differed in species composition from the abyssal VFZ and PRT and abundances were similarly low like the western VFZ. The Mid-Atlantic Ridge appeared not to be a barrier for the dispersal of the mostly lecithotrophic or planktotrophic larval stages of the reported molluscan species in this study.

1. Introduction

The benthic fauna on the continental slopes and in the deep-sea basins of the Atlantic Ocean has been sampled by marine scientists since the first discovery of life in the deep sea during the HMS Challenger expedition 1872-1876 (Thomson 1885) which led to the origin of deep-sea biology. The deep-sea marine life collected by HMS *Challenger* from the about 70 stations in the Atlantic, published and described as parts of the comprehensive zoological reports which include benthic Bivalvia (Smith 1885), Polyplacophora (Haddon 1886), Cephalopoda (Hoyle 1886), Scaphopoda and Gastropoda (Boog Watson 1886). Following was the first German deep-sea expedition on the *Valdivia*, sampling the eastern side of the Atlantic from the Faeroe Islands to the Antarctic continent, from which bivalves and gastropods were described by Thiele (1925) and Thiele & Jaeckel (1931). The Danish Deep-Sea expedition *Galathea* (1950-52), most famous for the discovery of the living Monoplacophora *Neopilina galathea* Lemche, 1957 (Lemche & Wingstrand 1959), sampled along the west African continental slope and across the north Atlantic from the Caribbean to Europe and the scientific reports included systematic account on deep-sea bivalves (Knudsen 1970). Clarke (1961) summarized some of the deep-sea findings (Gastropoda and Bivalvia) obtained during the abyssal trawls on board the *Vema* in the South-Atlantic. In the 1960ies and seventies, American, British and French expeditions sampled the Atlantic basins from the shelves, along the slopes to the deep-sea basins, enabling first Atlantic wide diversity and zoogeography assessments (Allen 2008). Sampling in the Atlantic hadal zones was more sporadic (Jamieson 2015), despite the first Atlantic hadal benthic fauna was being reported in 1901 from the North Atlantic Zeleniy Mys Trough (Koehler, 1909) and the Swedish *Albatross* expedition in 1948 sampling the Puerto Rico Trench (Nybelin, 1951). Belyaev (1989) reviewed the knowledge on the global deep-sea trench fauna, mentioning the hadal presence of molluscs in the Atlantic as aplacophorans from the South Sandwich Trench, a polyplacophoran from the Cayman Trench and cocculinid gastropods, scaphopods and bivalves in the general hadal area and Vinogradova et al. (2000) the benthic fauna in the

Atlantic Southern Ocean trenches and faults. The molluscan classes bivalves and gastropods served as the model taxa for analysing latitudinal (Rex et al. 1993) and bathymetric gradients (Rex et al. 2005) setting the paradigms of latitudinal gradients in the deep sea benthos and a source-sink system between bathyal and abyssal populations. At the start of this millennium the international Census of Marine Life project CeDAMar (Census of the Diversity of Abyssal Marine Life) led to recent expeditions with quantitative and qualitative sample collections (Stuart et al. 2008) and the first baseline studies on the biodiversity and abundance of selected benthic taxa and communities have been published (Brandt et al. 2011a, this volume and references therein). Despite these efforts, the knowledge on abyssal and hadal molluscan fauna of the deep Atlantic Ocean was patchy, depended on the molluscan class and especially scarce for the equatorial zone. The bivalves of the deep Atlantic were reviewed by Allen (2008) and his account of 468 species and 87 families in the Atlantic lists only 14 families of bivalves to be present in depth below 5000 m. Scarabino & Scarabino (2011) assessed the scaphopod fauna of the bathyal and abyssal Atlantic Ocean with 132 species of which the majority (90) were reported from the Western Atlantic and only 9 species are reported as ampho-Atlantic. To date no summarizing reviews for the deep-sea Atlantic gastropods, caudofoveates and solenogastres were available, only regional literature (e.g. Dall 1889, Leal 1991, Bouchet & Waren 1993, Leal & Harasewych 1999).

In late 2014 the expedition Vema TRANSIT with RV Sonne (SO237) set sail to investigate the geomorphology and abyssal benthic fauna along the Vema Fracture Zone (VFZ) and of the hadal Puerto Rico Trench (PRT) (Devey et al. 2015, Brandt et al. 2011a this volume, Devey et al. 2011b this volume). The biological objectives for this expedition were to study the macrofaunal taxon richness and abundances along an east-west transect of the VFZ, and to investigate if the Mid Atlantic Ridge serves as a barrier for faunal exchange between the eastern and western abyssal basins or if the Vema Transform serves as a migration route. Sampling in the hadal zone of the PRT gave the opportunity to study if its biodiversity differs from the abyssal Atlantic or has a source-sink relation with the abyssal fauna.

The study presented here is assessing the macrofaunal molluscan biodiversity collected by epibenthic sledges in the VFZ and the PRT. The expected results increased the faunistic knowledge on deep-sea Atlantic species, their abundances, assemblage compositions and distributions.

2. Material and methods

2.1. Study area and sampling

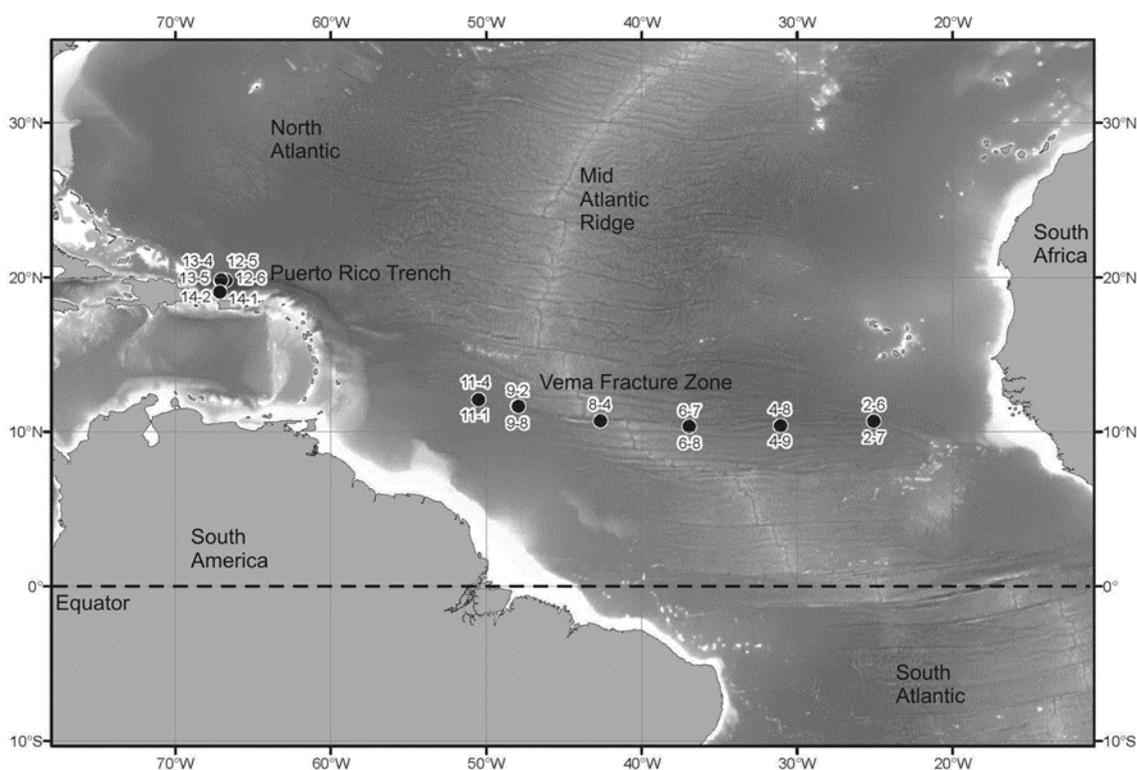
During the expedition SO237 “Vema-TRANSIT” of RV Sonne in 2014/15, a total of 17 camera-epibenthic sledge (C-EBS; Brandt et al., 2013) deployments were performed at nine sites (e.g. 2, 4, 6) with stations (e.g. 2-6, 2-7, 4-8) ranging from 4552 m – 8338 m (Table 1; Figure 1). At each site, with exception of site 8, two EBS hauls were taken to assess habitat homogeneity. In the VFZ sites were sampled at abyssal depth while in the PRT sites were sampled at abyssal and hadal depth.

The C-EBS held an epi- and a suprabenthic netsampler as well as 6000 m rated cameras, lights and environmental sensors (Brandt et al. 2013, Brandt et al. 201xb this volume). Each of these nets had an opening of 100 x 33 cm, net mesh size of 500 μ m, and cod ends were equipped with net-buckets containing 300 μ m mesh windows like in earlier used EBS samplers (Brandt & Barthel, 1995; Brenke, 2005). On deployment 1.5 times cable length to water depth were laid out for abyssal stations and 11000 m cable for hadal stations and then EBS was trawled with 1 kn for 10 minutes on the sea bed. The haul distances were calculated using the time and the speed (ships speed with 1 knot, and then winch speed with -0.5 m/sec.) until the C-EBS left the ground (Table 1) (also see Brandt et al. 201xb this volume). For comparison between stations abundance data were standardised to 1000 m² trawled area.

Once on the deck, the content of the cod-ends were immediately taken to the cool room and fixed in 96% pre-cooled (at -20°C) ethanol. The content of the epi- and supranets above the cod-ends was sieved over 500 μ m on deck and the residues were fixed in either pre-cooled (initially -20°C) ethanol or 4 % buffered formalin. The ethanol fixed samples were kept for at least 48 h in a -20°C freezer. The material was sorted on ice under stereomicroscopes initially into appropriate higher taxonomic levels (e.g. phyla, class, order). Molluscan specimens were sorted by the authors to morphospecies, identified to the lowest possible level and counts were made to determine abundance and species richness. For shelled molluscs we restricted analyses of molluscs-tissue containing specimens, empty or sediment filled shells were not counted.

Figure 1

Location of C-EBS stations along the VFZ and in the PRT.



For biodiversity analysis the supra- and epinet samples were pooled for every station and for comparisons between previous expeditions using EBS we show results from the entire net catch data as well as from the cod ends only.

2.2. Univariate measures of diversity and distribution of species

The number of morphospecies (SR) of caudofoveates, solenogastres, scaphopods, gastropods and bivalves in each sample was determined. Estimates for species diversity and evenness were made calculating for each station Shannon-Wiener index H' and Pielou's evenness index J' in PRIMER v6 (Clarke and Gorley, 2006). Individual-based interpolation (rarefaction) and extrapolation analyses (e.g. Cowell et al. 2012, Hsieh et al. 2016) were performed in iNEXT under standard settings (Chao et al. 2016) and resulting interpolation and extrapolation curves for all station with exception of station 12-6, which had inadequate sample size, were compared.

Species only found at a single station were referred to as 'uniques' and species found at only 2 stations as 'duplicates' following the terminology of Colwell and Coddington (1994). The

term ‘singleton’ referred to morphospecies that were represented by only one individual overall and ‘doubletons’ refers to represented by only two individuals. The term ‘range size’ referred to the number of stations at which a morphospecies was found within the studied sites, i.e. not to the entire geographical range of (morpho)species (Gaston et al., 1997).

Following Brandt et al. (this volume) the term “common” was used for a number of molluscan specimens per species of ~50 across all stations, with the term “rare” referring to singletons, doubletons or <10 molluscan specimens per station and across all stations.

2.3. Multivariate analyses

PRIMER v6 (Clarke and Gorley, 2006) was used to determine the overall molluscan assemblages, as well as the class assemblages separately. The Bray-Curtis similarity coefficient was applied to non-transformed abundance data of all taxa obtaining a similarity matrix (Clarke and Gorley, 2006). Hierarchical clustering with group-averaged linking and non-metric multidimensional scaling (MDS) was then performed using these matrixes. One-way ANOSIM tests were performed to investigate the differences between groups of stations.

Table 1

Stations list of the C-epibenthic sledge samples from VEMA Transit, molluscan abundance and diversity indices.

Station	Date	Depth (m)	Lat° N	Long° W	Haul length (m)	N	N /1000m	SR	J'	H'		
SO237			Start ship	End ship	Start ship	End ship				log e		
2-6	20/12/2014	5520	10°43.78'	10°43.79'	25°03.72'	25°03.73'	1846	22	12	9	0.9225	2.027
2-7	20/12/2014	5507	10°42.891'	10°42.92'	25°03.21'	25°03.167'	2020	132	65	25	0.9171	3.056
4-8	27/12/2014	5725	10°25.62'	10°25.62'	31°04.40'	31°04.37'	1750	291	166	21	0.7162	2.18
4-9	27/12/2014	5733	10°25.65'	10°25.66'	31°02.98'	31°02.98'	1900	196	103	24	0.7922	2.518
6-7	02/01/2015	5079	10°21.82'	10°21.83'	36°55.06'	36°55.06'	1980	92*	46	18	0.9003	2.651
6-8	02/01/2015	5127	10°22.65'	10°22.66'	36°55.35'	36°55.35'	1400	146	104	29	0.7773	2.669
8-4	06/01/2015	5178	10°43.00'	10°43.00'	42°39.73'	42°39.73'	1750	75*	43	12	0.6919	1.719
9-2	11/01/2015	4986	11°40.73'	11°40.45'	47°58.03'	47°59.00'	786	8	10	7	0.9796	1.906
9-8	12/01/2015	5001	11°39.36'	11°39.36'	47°53.99'	47°53.97'	1613	57	35	18	0.8789	2.588
11-1	14/01/2015	5088	12°05.84'	12°05.81'	50°27.97'	50°27.96'	1320	20	15	13	0.9584	2.458
11-4	14/01/2015	5108	12°04.83'	12°04.82'	50°28.14'	50°28.14'	1416	18	13	9	0.9253	2.033
12-5	20/01/2015	8338	19°46.85'	19°46.85'	66°50.02'	66°49.99'	1611	22	14	3	0.3346	0.3676
12-6	21/01/2015	8336	19°48.601'	19°48.605'	66°45.130'	66°45.120'	602	7	12	1	-	0
13-4	23/01/2015	8317	19°42.12'	19°47.13'	67°05.79'	67°05.79'	750	27	36	3	0.5205	0.5718
13-5	23/01/2015	8042	19°50.118'	19°50.14'	67°02.617'	67°02.60'	840	27	32	3	0.6177	0.6786
14-1	23/01/2015	4552	19°02.097'	19°02.11'	67°09.247'	67°09.43'	764	86	113	16	0.8071	2.238
14-2	23/01/2015	4925	19°04.67'	19°04.67'	67°07.77'	67°07.75'	968	107	111	22	0.8313	2.57

Shannon–Wiener diversity H' was calculated using $\log e$ and the evenness index J' of Pielou was calculated. N: number of molluscan specimens in haul, N/1000 m: abundance of molluscan specimens per 1000 m² area, SR: number of morphospecies.

3. Results

The 17 C-EBS stations in the VFZ (11 stations) and PRT (6 stations) yielded a total of 1333 specimens and 64 morphospecies of the Caudofoveata (86 spec/7 spp), Solenogastres (180/7), Gastropoda (67/24), Bivalvia (686/22) and Scaphopoda (314/4) (Figure 1, Table 2). Overall Bivalvia were most rich and abundant closely followed by scaphopods in abundance, but with far lower number of species (Table 2). The benthic gastropods were as rich as bivalves but were extremely rare in abundance while caudofoveates and solenogastres showed low species numbers and generally low abundances. Monoplacophorans, polyplacophorans and cephalopods were not collected at all. The 11 stations in the VFZ yielded 1057 specimens and 53 morphospecies of the Caudofoveata (81 spec/5 spp), Solenogastres (120/5), Gastropoda (37/20), Bivalvia (506/18) and Scaphopoda (313/4) while the six stations in the PRT yielded 276 specimens and 32 morphospecies of the Caudofoveata (5 spec/4 spp), Solenogastres (60/5), Gastropoda (30/8), Bivalvia (180/14) and Scaphopoda (1/1) (Table 1, Supplement Table 1).

Comparison between all net and cod-end only data showed that for caudofoveates, solenogastres, gastropods and bivalves more than half of all live collected specimens came from the cod-ends while in the scaphopods two thirds of the specimens were present in the net overflow samples (Table 2). Regarding species richness, entire net samples added morphospecies that were not present in the cod ends.

Table 2

Numbers of specimens and morphospecies per class and station for all net data and for cod ends only.

Station SO237	Caudofoveata		Solenogastres		Scaphopoda		Gastropoda		Bivalvia	
	N	SR	N	SR	N	SR	N	SR	N	SR
All data										
2-6	1	1	11	3	0	0	0	0	10	5
2-7	19	3	20	4	14	3	10	6	69	10
4-8	28	1	10	5	188	4	5	4	60	7
4-9	23	4	12	3	77	4	3	3	81	10
6-7	4	1	15	2	12	3	0	0	61	12
6-8	4	2	20	3	3	3	8	7	111	14
8-4	0	0	6	2	6	2	2	2	61	6
9-2	2	1	2	2	0	0	1	1	3	3
9-8	0	0	18	3	6	2	5	4	28	9
11-1	0	0	2	2	6	3	0	0	12	8
11-4	0	0	4	2	1	1	3	3	10	3
12-5	0	0	0	0	0	0	0	0	22	3
12-6	0	0	0	0	0	0	0	0	7	1
13-4	1	1	0	0	0	0	0	0	26	2
13-5	0	0	0	0	0	0	1	1	26	2
14-1	3	3	38	3	1	1	13	5	31	4
14-2	1	1	22	4	0	0	16	5	68	12
Sum	86	7	180	7	314	4	67	24	686	22
Cod ends										
2-6	1	1	10	3	0	0	0	0	10	5
2-7	11	3	11	4	7	1	2	2	23	6
4-8	10	1	6	3	13	4	5	4	3	3
4-9	14	4	10	3	47	4	0	0	15	5
6-7	4	1	15	2	12	3	0	0	59	11
6-8	2	1	17	3	3	3	0	0	58	11
8-4	0	0	6	2	6	2	1	1	44	4
9-2	2	1	2	2	0	0	1	1	3	3
9-8	0	0	18	3	6	2	3	3	12	5
11-1	0	0	2	2	1	1	0	0	3	2
11-4	0	0	4	2	1	1	3	3	6	2
12-5	0	0	0	0	0	0	0	0	10	2
12-6	0	0	0	0	0	0	0	0	3	1
13-4	1	1	0	0	0	0	0	0	5	1
13-5	0	0	0	0	0	0	0	0	7	2
14-1	3	3	38	3	1	1	13	5	26	4
14-2	1	1	21	3	0	0	11	2	55	8
Sum	49	7	160	6	97	3	39	17	342	19

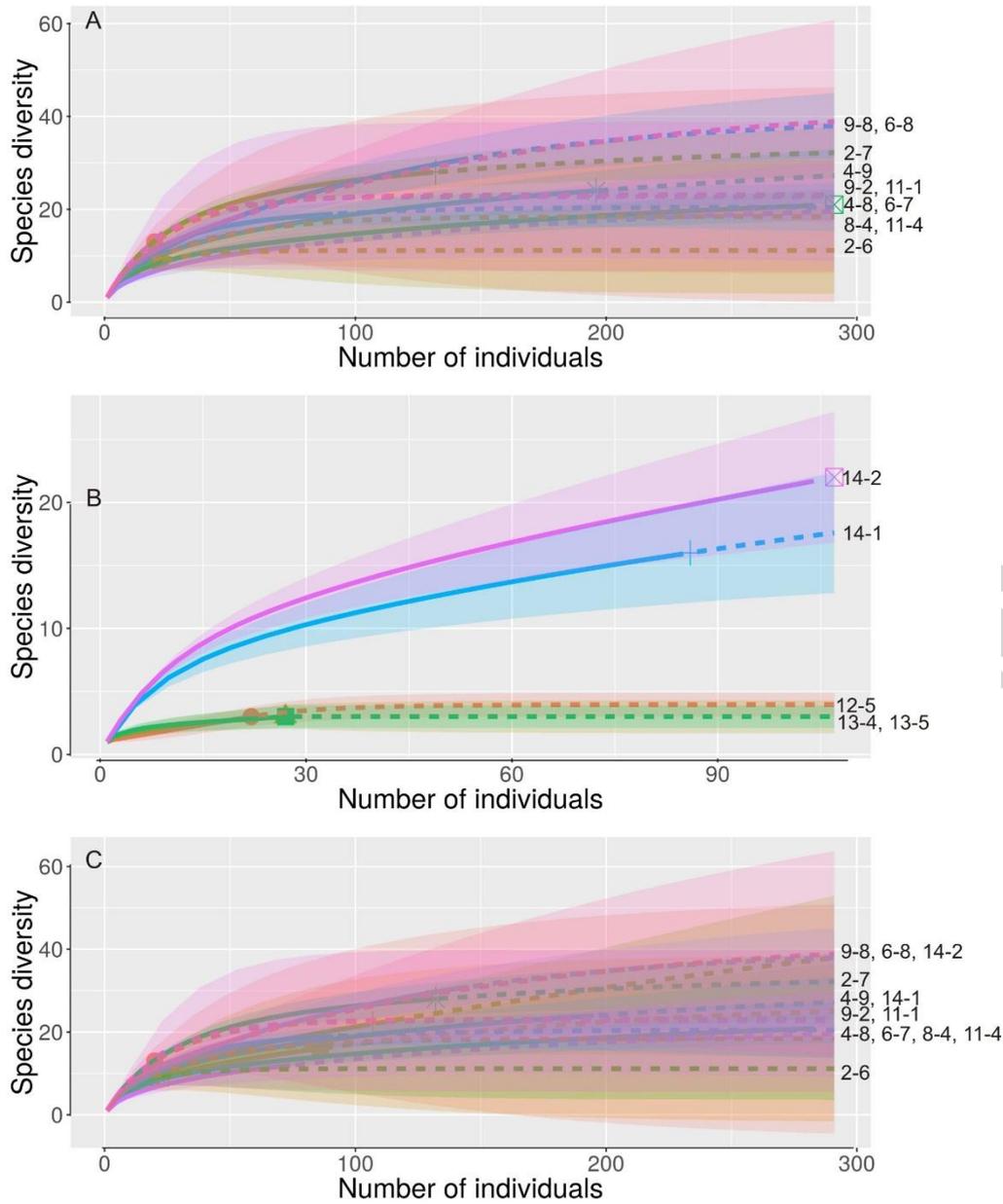
N: number of specimens in haul, SR: number of morphospecies.

3.1. Species richness

Morphospecies richness between stations varied from 1 to 29 species (all data; 1 to 18 codends only) and most morphospecies were found at station 6-8 with 29 (6-8 for cod ends with 18) species (Table 1, 2). Morphospecies overlap between VFZ and PRT varied between taxa; while only one of four scaphopod and four of 24 gastropod morphospecies were found in both areas, two of seven morphospecies of caudofoveates, three of seven solenogastres and eleven of 22 bivalves were present in VFZ and PRT (Supplement Table 1).

Figure 2

Individual-based interpolation (rarefaction) and extrapolation curves for stations: A) Vema Fracture Zone, B) Puerto Rico Trench, C) abyssal stations only.



Shaded (or coloured in on-line version) areas represent 95% unconditional confidence intervals under multinomial model. Solid line – interpolation, broken line – extrapolation.

Species richness evaluated through individual-based interpolation (rarefaction) and extrapolation curves (Figure 2) showed clusters of curves having largely overlapping unconditional confidence intervals in the VFZ and at abyssal depth (Figures 2A, C). In the PRT the hadal stations showed markedly different values from the abyssal stations (Figure 2B) as their unconditional confidence intervals did not overlap.

The majority of species was rare with 21 of the 64 morphospecies being ‘uniques’, of which 15 are even ‘singletons’, ten morphospecies being ‘duplicates’ and eight morphospecies being ‘doubletons’ which occurred at one or two stations with a total of two individuals. (Table 3). The number of common species was low, with none of gastropods, only one morphospecies of caudofoveates, two of solenogastres, and five of 22 bivalves but three out of four scaphopod morphospecies (Supplement Table 1). The most common morphospecies were Solenogastres sp. 1 occurring at eleven stations and the bivalves *Ledella* sp. and *Malletia* sp. occurring at ten of the 17 stations (Table 3).

Table 3

Density and range of the most abundant morphospecies per taxon at the 17 stations. Number of uniques, duplicates and singletons are given. Presence in VFZ or PRT marked.

Taxonomic group	Species	N	Range size	VFZ	PRT
Caudofoveata	Uniques	2	1		2
	Duplicates	2	2	2	1
	Singletons	2	1		2
	Doubletons	1	2	1	1
	Prochaetodermatidae sp.	56	4	4	
	Caudofoveata sp. 3	12	4	4	
	Caudofoveata sp. 2	7	4	2	2
Solenogastres	Uniques	2	1		2
	Duplicates	1	2	1	
	Singletons	1	1		1
	Doubletons	1	1		1
	Solenogastres sp. 1	57	11	11	
	Solenogastres sp. 3	56	9	7	2
	Solenogastres sp. 4	40	7	5	2
Scaphopoda	Uniques	-	1		
	Duplicates	-	2		
	Singletons	-	1		
	Doubletons	-			
	<i>Cadulus</i> sp.	139	9	9	

	Dentaliidae sp.	76	5	5	
	<i>Striopulsellum</i> sp.	56	5	5	
Gastropoda	Uniques	14	1	12	2
	Duplicates	6	2	4	3
	Singletons	11	1	10	1
	Doubletons	6	1-2	4	4
	? <i>Pseudococculina</i> sp.	18	2		2
	<i>Choristella agulhasae</i>	7	5	3	2
	? Skeneidae sp.	6	3	2	1
Bivalvia	Uniques	3	1	1	2
	Duplicates	1	2	1	1
	Singletons	1	1	1	1
	Doubletons	-			
	<i>Malletia</i> sp.	125	10	9	1
	<i>Ledella</i> sp.	79	10	8	2
	<i>Myonera</i> sp.	77	5		5

N: number of morphospecies, PRT: Puerto Rico Trench, VFZ: Vema Fracture Zone.

3.2. Abundance and composition

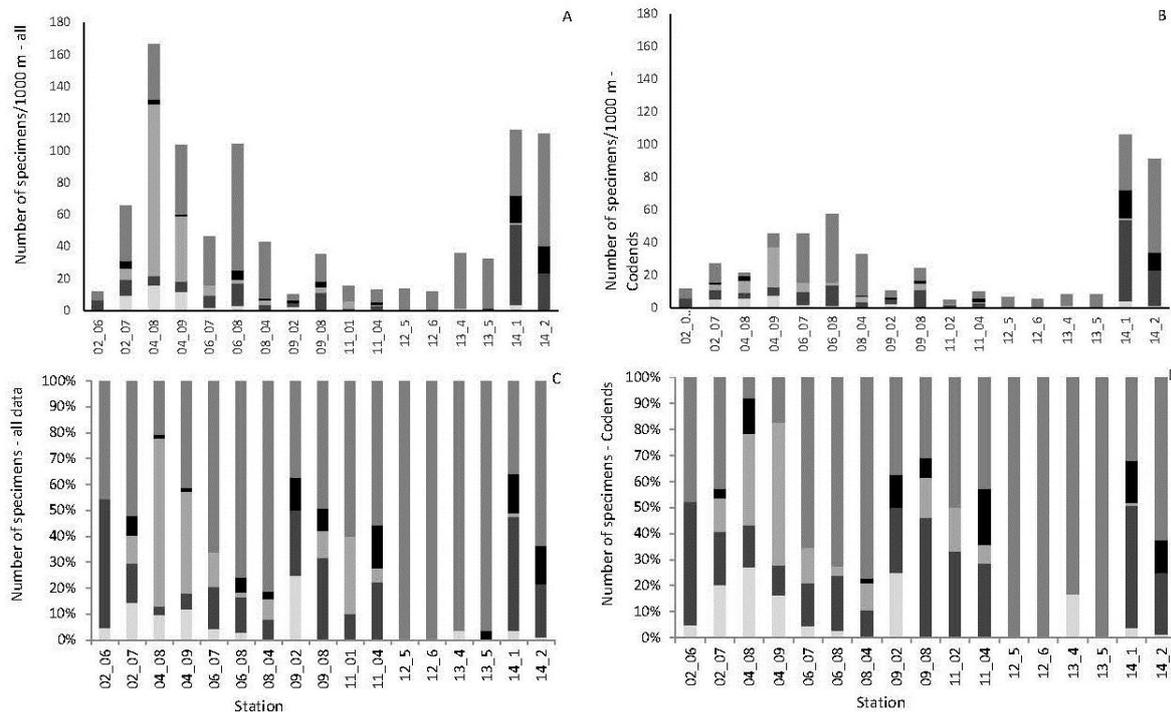
Analysing all data, the scaphopod *Cadulus* sp. of the family Pulsellidae was the most abundant species with a total of 139 specimens followed by the bivalves of the genus *Malletia* Desmoulins, 1832 with 125 specimens and the genus *Ledella* Verrill & Bush, 1897 with 79 specimens (Table 3).

The standardised abundance of specimens for comparisons between stations varied from 11 to 167 (all data; 5 to 106 codends only) and most individuals were found at station 04-08 with 167 specimens (106 specimens at 14-1 codends only) (Figures 3 A, B). The stations in the eastern side of the VFZ (sites 2 to 6) presented higher abundances of benthic molluscs than the stations at the Mid Atlantic Ridge (site 8) or western VFZ (sites 9-11). The abyssal stations in the PRT (site 14) presented similar abundances to the eastern VFZ while the hadal stations (sites 12 to 13) held lower standardised abundances similar to those in the western

VFZ. The standardised abundances showed a dominance of infaunal groups, especially bivalves and scaphopods, while abundances of epifaunal groups like gastropods were low or absent as in the case of Monoplacophora and Polyplacophora. The abyssal stations in the PRT (stations 14-1, 14-2) showed high standardised abundances of Solenogastres in relation to the overall ones.

Figure 3

Specimen abundances per station: A) Standardised (1000 m²) all nets, B) standardised (1000 m²) cod ends only, C) relative all nets, D) relative cod ends only.



Caudofoveata ■, Soleogastres ■, Scaphopoda ■, Gastropoda ■, Bivalvia ■

The relative abundances of individuals (Figures 3 C, D) within the five molluscan classes varied between stations. In general bivalves were dominant as shown at 11 of 17 stations with >50% of specimens (at eight stations for cod ends). Scaphopods dominated relative

abundances at stations 04-08 and 04-09, both stations showing highest specimen numbers, too.

The multivariate analyses of assemblage structure (MDS plots) showed a significant separation of the hadal stations (black triangles) with all molluscan taxa combined (Figure 4A, Table 4) as well as for individual taxon plots (Appendix Figure 1 A-E). The multivariate analyses of the abyssal stations only showed an apparent separation of the stations by area with a 2D stress of 0.12 (Figure 4B) and a 3D stress of 0.08 (data not shown).

Figure 4

MDS plot on all molluscan taxa for A) factor depth zone of complete dataset, B) factor area of abyssal stations.

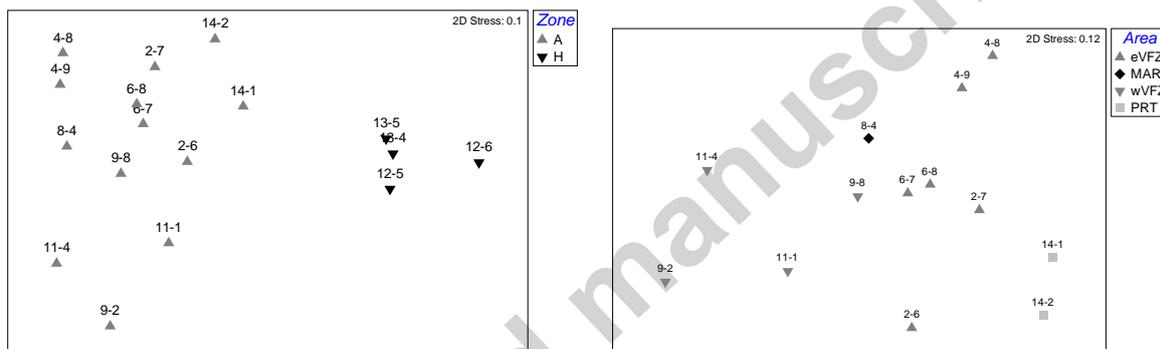


Table 4

One-way ANOSIM analysis

	R	Significance
Global Test	Statistic	Level %
Depth	0.886	0.1
Area, abyssal stations only	0.586	0.2
Pairwise Tests	R	Significance
Groups	Statistic	Level %
eVFZ, MAR	-0.022	42.9
eVFZ, wVFZ	0.615	1
eVFZ, PRT	0.573	3.6
MAR, wVFZ	0.5	20
MAR, PRT	1	33.3

4. Discussion

The macrofaunal Mollusca presented in this study were behind the Crustacea and Annelida the third most abundant and prominent phylum present in the C-EBS samples collected during the Vema TRANSIT expedition (Brandt et al. 201xb this volume). The studied malacofauna comprises of five of the eight molluscan classes, Caudofoveata, Solenogastres, Bivalvia, Gastropoda and Scaphopoda, while Cephalopoda, Monoplacophora and Polyplacophora were not present. Highly mobile squids and octopuses are rarely collected by EBS deployments (e.g. Linse 1999, Brandt et al. 2013, Jörger et al. 2014) as they are able to avoid the slowly towed sledge by escaping. Monoplacophora and Polyplacophora, which can be collected with fine-meshed gear like the EBS (Linse 1999, Schiaparelli et al. 2014, Brandt et al. 2015), are often rare or absent in abyssal and hadal stations (Brandt et al 2013, Brandt et al. 2014, Jörger et al. 2014). Schwabe (2008) summarized the records of deep abyssal and hadal of these two classes, reporting only two monoplacophoran species from the Atlantic, *Rokopella brummeri* [= *Veleropilina brummeri* (Goud & Gittenberger, 1993)] from 2162 m on the northern MAR, and *Neopilina rebainsi* Moskalev, Starobogatov & Filatova, 1983 from 4660-5630 m south of the Falkland Islands. Abyssal and hadal polyplacophorans are known with *Leptochiton alveolus* (M. Sars MS, Lovén, 1846) of Spain and three species of *Ferreiraella* from the Caribbean, of which *Ferreiraella caribbensis* Sirenko, 1988 from 6740 m in the Cayman Trench is noteworthy here. A further polyplacophoran, *Stenosemus exaratus* (G.O. Sars, 1878), was more recently confirmed inhabiting abyssal depths in the North Atlantic (Allcock & Schwabe 2013). The review of the deep Atlantic bivalves comprising 468 species and 87 families listed only 14 families deeper than 5000 m Allen (2008). The 11 bivalve families and 23 morphospecies reported from the Vema-TRANSIT expedition appear to represent the reported bivalvian fauna well. In their assessment of the bathyal and abyssal scaphopod fauna in the Atlantic Ocean Scarabino & Scarabino (2011) listed with 132 species of which the majority (90) are reported from the Western Atlantic and only 7 species are reported as amphi-Atlantic. All four abyssal scaphopod species reported here from the VFZ show amphi-Atlantic distributions and are either widening the distribution records of described species or confirm Scarabino & Scarabino's (2011) statement that the deep-water realm and its scaphopod diversity are far from adequately inventoried. To date no summarizing reviews for the deep-sea Atlantic gastropods, caudofoveats and solenogastres

are available, only regional literature (e.g. Dall 1889, Leal 1991, Bouchet & Waren 1993, Gil-Mansilla et al. 2008), especially for the north-east Atlantic (Bouchet & Warén, 1980, 1985, 1993). Information on caudofoveates and solenogastres occurrence is available (e.g., Scheltema & Ivanov 2000, García-Álvarez & Salvini-Plawen 2007 and literature therein), but not applicable for the present analysis as the original sources hardly deal with quantitative composition, and the present identification of the material requires a more detailed morphological study.

Further in-detail morphological and molecular taxonomic analyses on the current morphospecies, especially on the bivalve taxa with few morphological shell characters, are required for species identifications to enable species-level biogeographic analyses.

4.1. Species richness

Morphospecies richness for the molluscs collected by C-EBS along the VFZ and in the PRT ranged from 7 to 29 species at the abyssal stations and 1 to 3 species at the hadal ones. The analysis of species richness by rarefaction methods (Gotelli and Ellison, 2013) enabled comparisons between stations despite sampling effort constraints. Species richness at stations in abyssal depth of the VFZ and PRT did not differ within and between these two areas while hadal stations showed significantly lower species richness. The morphospecies richness appeared low in comparison to the species richness found in comparable abyssal EBS stations. At present 24 of the 53 molluscan morphospecies present at the stations along the VFZ were found in its eastern and western parts, crossing the Mid-Atlantic Ridge. Stuart & Rex (2009) listed from a 5216 m station in the Argentine Basin alone 35 gastropod species, which is even higher than our total species number. During the ANDEEP I & II expeditions to the Atlantic sector of the Southern Ocean, bivalve and gastropod species richness at abyssal stations ranged from 7 to 31 species (Linse 2004, Schwabe et al. 2007) while the collected aplacophorans and scaphopods have yet to be identified to species. Jörger et al (2014) analysing the macrofaunal malacofauna of the abyssal EBS stations in the South Atlantic Polar Front region reported overall species richness for the taxa same classes as reported here ranging from 8 to 29 species. Schrödl et al. (2011) examining the gastropods from the DIVA I & II expeditions documented a gastropod diversity from the Guinean to the Cape Basin ranging from 1-8 species at abyssal depth and highlighted that obviously no faunal overlap exists with the previously examined (Schwabe et al. 2007) Antarctic deep-sea

gastropods. Contrasting data from abyssal depths in the Angola Basin are available from Stuart & Rex (2009), who listed 14-20 gastropod species in about 4500 m.

Table 5

Species richness of molluscan taxa collected at abyssal EBS stations. n/a – data not available while taxon present

	Vema TRANSIT VFZ + PRT	ANDEEP I-II SA-SO	SYSTCO II PF-SA	DIVA I-II eSA
abyssal species richness	7-29	7-31	8-29	1-8
Caudofoveata	7	n/a	3	n/a
Solenogastres	6	n/a	2	n/a
Scaphopoda	4	n/a	7	n/a
Gastropoda	24	21	24	24
Bivalvia	22	37	22	n/a

Vema TRANSIT – this study, ANDEEP I-II - Linse 2004, Schwabe et al. 2007, SYSTCO II – Jörger et al 2014, DIVA I-II – Schrödl et al. 2011

The overall species richness patterns seen at the Vema TRANSIT stations are in line with the current knowledge on abyssal molluscan species diversity collected by EBS with gastropods and bivalves being the more speciose classes (Table 5) and gastropods species been often present as singletons and uniques (this study, Schwabe et al. 2007, Jörger et al. 2014). The species composition in bivalves is comparable to that reported from the Biovema expedition (Allen, 2008). Remarkable is the finding of deep-sea limpets exclusively in the PRT. Some of the specimens were fairly attached to plant remains, and an accumulation of such biogene substrata is well recorded for this region (Moore 1963). Leal & Harasewych (1999) already showed the strong association of these gastropods with plant remains, and the present data may further underline such a local restriction. In contrast we do not observed morphological differences between Antarctic populations and recent findings of *Choristella agulhasae* but a genetic analysis is still outstanding to tests, whether these populations belong to a single species or reflect genetically distinct local populations.

The presented analysis of molluscan species richness and taxon composition based morphospecies did not show the Mid Atlantic Ridge to be a barrier for species dispersal as no differences for the eastern and western VFZ stations were found. This finding was in line with the results of the diversity analysis of the overall macrofaunal taxa collected by C-EBS

during VEMA-TRANSIT (Brandt et al. 201xb, this volume) but different to the patterns shown by morphospecies of polychaetes (Guggolz et al. 201x, this volume). Guggolz et al. (201x, this volume) discussed that the abiotic disparities between the eastern and western VFZ might be causing the differences in family and species composition. First molecular studies on selected deep-sea isopod taxa collected during VEMA-TRANSIT revealed genetic differences in morphospecies collected from the eastern and western VFZ (Bober et al. 201x, this volume, Brix et al. 201x, this volume, Kaiser et al. 201x, this volume, Riehl et al. 201x, this volume). Brix et al. (201x, this volume) concluded based on COI and 16S sequences from 195 desmosomatid and nannoniscid specimens which were assigned to 69 species following ABGD analysis that a horizontal limitation of species distribution is present and that only eight of the analysed species crossed the complete VFZ. Several of the species revealed had been unknown and are subsequently described in Brix et al. (201x, this volume) and Kaiser et al. (201x, this volume). The comparative molecular analysis (16S, 18S) of specimen-rich, VFZ crossing species of a swimming desmosomatid versus a burrowing macrostylid isopod revealed that no haplotypes were shared between the eastern and western sides (Bober et al. 201x, this volume). This finding was further supported by Riehl's (201x, this volume) multigene analyses (16S, 18S, COI) for macrostylid isopods, which showed clear differences in eastern and western VFZ as well as PRT molecular operational taxonomic units but also that taxa with restricted dispersal can have wide distribution ranges. Future molecular species delimitation studies on the molluscan taxa will reveal if the identified morphospecies show genetic marker differences in populations living across the Mid-Atlantic Ridge.

4.2. Abundance and composition

The abyssal macro-molluscan standardized abundances were higher on the eastern VFZ than on the western side. This might be caused by the differences in the environmental settings of the eastern and western side. In the east the sediments were fine and muddy or even consisted of foraminiferans while in the west the sediments were characterized by manganese crusts or even nodules (Devey et al. 201x this volume, Brandt et al. 201xb, this volume). The high numbers of foraminiferan eating molluscan species, e.g. scaphopods and anomalodesmatan bivalves, present in the eastern VFZ might be due to this. On the other hand it is hard to understand, why the numerous hard substratum investigated at the western

site of the VFZ yielded almost none epibenthic organism. Manganese nodules are shown to serve as suitable substrates for Polyplacophorans and Monoplacophorans for example (e.g., Paul 1976, Schwabe 2008).

The comparative discussion of the standardized abundances of the macrofaunal molluscs collected during VEMA TRANSIT faced the difficulty that no comparable abundance data from previous deep-sea EBS deployments are available. At previous expeditions, molluscan classes were distributed to taxonomists for in detail identification before morphospecies and their abundances were assessed, disabling a molluscan-wide composition analyses as done in this study. For ANDEEP I-II from the abyssal Atlantic sector of the Southern Ocean, only standardized abundances from bivalves (Linse, 2004) and gastropods (Schwabe et al. 2007) were available. Pooling their standardized abundances, they varied between 1 and 52 specimens per 1000 m² trawls. Jörger et al. (2014) reported standardised abundances for abyssal gastropods of 0.77 to 2.64 specimens per 1000 m² trawls for the South Atlantic Polar Front region and Schrödl et al. (2011) standardised abundances for abyssal gastropods of 0.25 to 2.19 specimens per 1000 m² trawls for the Guinea, Angola and Cape basin in the southeastern Atlantic. Linse (1999) published on the macrofaunal molluscs of the Magellanic Beagle channel collected in 25 – 665 m depth and abundances standardized to 1000 m² trawls varied from 3 to 38.025 specimens. Eleven of the 18 EBS stations accounted more than 1000 specimens of caudofoveates, solenogastres, polyplacophorans, scaphopods, gastropods and bivalves, but then these stations located within an islands and channel systems were influenced by land-based nutrient run-off and phytoplankton blooms.

5. Conclusions

This presented study on the abundances and species richness of the macrofaunal Mollusca increased the knowledge on the diversity of the Atlantic deep-sea fauna. The abyssal macro-molluscan species composition based on morphospecies did not varied between the eastern and western Atlantic sides of the Vema Fracture Zone while their reported abundances are higher on the eastern side. For these abyssal macrofaunal molluscs, the Mid-Atlantic Ridge appeared not to be a barrier for the dispersal of their mostly lecithotrophic or planktotrophic and not brooded or direct developed larval stages. This finding based on morphology will need to be tested with molecular marker analysis. The abyssal stations in the Puerto Rico Trench resembled the species composition of the VFZ while the molluscan species present in

hadal depth differed from the abyssal VFZ and PRT. Further in-detail morphological and molecular analyses will have to confirm the taxonomic status, distribution ranges and biogeographic affinities of the current morphospecies. The present study while referring to previous standardized EBS analyses clearly demonstrated that an inhomogeneity does exist for species richness and also for abundances of molluscan classes via deep-sea basins of the Atlantic Ocean. Such differences must not necessarily reflect latitudinal or bathymetrical gradients (e.g. Rex et al. 1993, 2005), but may be influenced by a broad set of factors, hardly or not compared in earlier (and present) analyses (e.g., filling level of codends and nets; directions of bottom currents; predatory pressure, reproduction cycles, nutrient introduction in a particular area etc.). Adding a further contribution to the Atlantic Oceans faunal composition, we are still far away from an understanding of true deep-sea molluscan diversity and abundance.

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