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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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## 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 m<sup>2</sup> 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 and Jaeckel (1931). The Danish Deep-Sea expedition *Galathea* (1950–52), most famous for the discovery of the living Monoplacophora *Neopilina galathea* Lemche, 1957 (Lemche and 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

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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. 201xa, 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 and 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 & Warén 1993; Leal and 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, 2015; Brandt et al. 201xa, this volume; Devey et al. 201x, 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 sledge 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; Fig. 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 100×33 cm, net mesh size of 500 µm, and cod ends were equipped with net-buckets containing 300 µm mesh windows like in earlier used EBS samplers (Brandt and 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 m<sup>2</sup> 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 µm 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.

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. Colwell 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.

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 m<sup>2</sup> 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) (Fig. 1, Table 2). Overall Bivalvia were most rich and abundant closely followed by

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