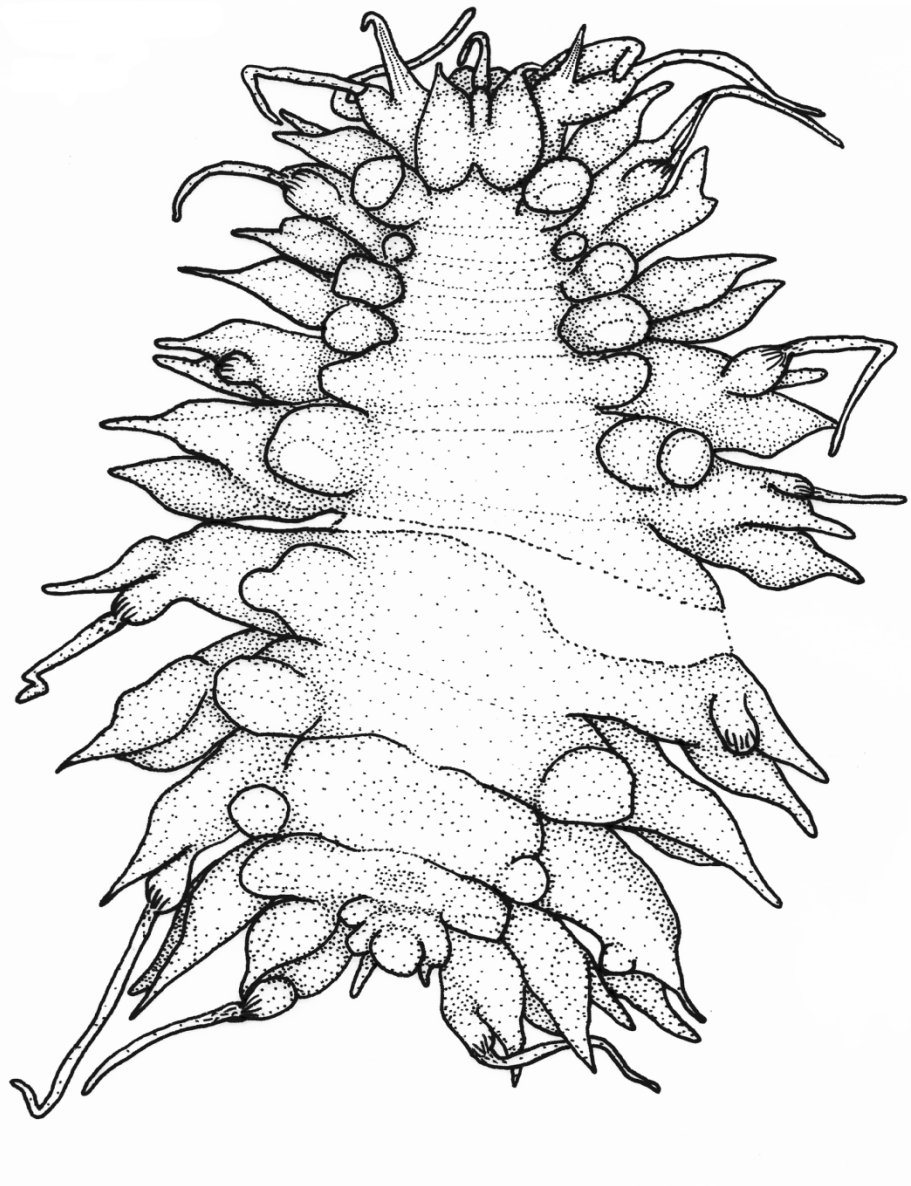
DISSERTATION

Diversity and distribution patterns of deep-sea polychaetes (Annelida) in the tropical Atlantic



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Diversity and distribution patterns of deep-sea polychaetes (Annelida) in the tropical Atlantic

DISSERTATION

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CHAPTER 7

CHAPTER 1

Introduction

Introduction

I. The deep sea

For a long time, the deep sea was considered to be a monotonous environment, with no light and most probably uninhabitable for any life (e.g. McClain and Hardy 2010, Ramirez-Llodra et al. 2010). This general view did not fundamentally change until the early nineteenth century (Snelgrove and Smith 2002), followed by the first systematic sampling of this unexplored ecosystem initiated about 147 years ago with the Challenger Expedition (Gage and Tyler 1992). Decades of improving and refining sampling techniques and methods drastically changed the original assumptions towards recognizing that the deep sea is the largest ecosystem on earth with high faunal diversity and a complex ecology (e.g. Hessler and Sanders 1967, Sanders and Hessler 1969, Grassle and Maciolek 1992, Snelgrove and Smith 2002, Rex and Etter 2010).

The deep sea constitutes around 90 % of the oceans covering two thirds of the planet's surface (Ramirez-Llodra et al. 2010, Harris et al. 2014). Despite the vast expanse of the deep sea, only a small proportion (< 0.1 %) has been studied and sampled to date (e.g. Ramirez-Llodra et al. 2010, Rex and Etter 2010, Danovaro et al. 2017).

In general, the parts of the oceans starting at the edge of the continental margins and lying below 200 m depth are defined as deep sea (Gage and Tyler 1992). This area again is divided in three depth zones, the bathyal (~200 – 4,000 m), the abyssal (4,000 – 6,000 m) and the hadal (> 6,000 m) (Jamieson 2015). The benthic bathyal accounts for around 15 % of the World Ocean area (Harris et al. 2014) and comprises continental slopes and rises, but also seamounts and mid-ocean ridges (Zezina 1997). The bathyal zone is described to be heterogeneous regarding factors like sediments, hydrostatic pressure, temperature and food-supply, mainly caused by the steepness of the habitat, decreasing towards the abyssal (Thistle 2003, Ramirez-Llodra et al. 2010, Harris et al. 2014). Almost independently from processes taking place in the benthic zones, the bathypelagic represents an ecosystem, covering a large proportion of the deep ocean volume (~75 %) (Robison 2004, Ramirez-Llodra et al. 2010). The deepest parts of the ocean, the hadal, is represented almost exclusively by trenches (Jamieson et al. 2010, Jamieson 2015) and accounts for less than 1 % of global benthic deep-sea areas (Harris et al. 2014). Usually, hadal trenches are V-shaped, very narrow with steep slopes up to 45° or more (Ramirez-Llodra et al. 2010, Jamieson

2015) and an extreme topographic complexity (Beliaev and Brueggeman 1989), resulting in a heterogeneous environment. Sediment, plant debris and surface derived material is transported downwards the steep slopes, accumulating along the trench axis (Danovaro et al. 2003, Romankevich et al. 2009), with the trench acting like a sedimentation tank, physically capturing the material at these depths and resulting in high sedimentation rates (Jamieson et al. 2010, Jamieson 2015). Despite the heterogeneous environment, factors like temperature are described to be stable (Beliaev and Brueggeman 1989), mainly affected by the hydrostatic pressure that is one of the most important factors in such depths (Jamieson 2015). The largest component of the deep sea are the abyssal basins (~85 % of global ocean's surface area, Harris et al. 2014), mainly represented by extensive abyssal plains (Ebbe et al. 2010, Ramirez-Llodra et al. 2010). These abyssal plains are interconnected and remarkably flat, on average with less than 1 m change in heights over a distance of 1 km, with a thick layer of fine, soft sediment covering most of the underlying topography (Smith et al. 2008, Ramirez-Llodra et al. 2010, Harris 2012). Although it has to be considered that the abyssal soft sediment is derived from terrigenous particles (weathering rocks), which are transported into the ocean through rivers and wind resulting in a decreasing rate of supply and particle size with increasing distance from land (Thistle 2003). Even though the abyssal appears monotonous, it is a dynamic environment, experiencing regular and episodic disturbances like tidal currents and benthic storms (e.g. Tyler 1988, Ebbe et al. 2010, McClain and Hardy 2010, Ramirez-Llodra et al. 2010). The abyssal plains are interrupted by geological features like mid-ocean ridges, seamounts and abyssal hills, formed by geologically active zones (e.g. Harris 2012). These geological features are representing among others (e.g. manganese nodules, mollusc shells, mussel beds and corals) hard-bottom habitats (Thistle 2003, Young 2009, Ramirez-Llodra et al. 2010). One main factor all three zones of the deep sea have in common is the absence of light for photosynthesis, resulting in heterotrophic environments (Thistle 2003, Ramirez-Llodra et al. 2010). Accordingly, energy in the deep sea is extremely limited and dependent on primary production in the euphotic zone, with some exceptions like hydrothermal vents (Thistle 2003, Smith et al. 2008, Ramirez-Llodra et al. 2010). The so-called particulate organic carbon flux is thought to be mainly responsible for the food availability in the abyss, compromising a complex mixture of organic material and detritus (e.g. Smith and Demopoulos 2003, Buesseler et al. 2007, Smith et al. 2008). Other abiotic factors are relatively constant. The water in the deep sea is lying under a thermocline and temperatures are slightly varying around 2 °C with some exceptions, the salinity is almost always ~35‰ and in

areas with constant circulating currents the dissolved oxygen is near saturation (5–6 ml l-1) (Thistle 2003, Ramirez-Llodra et al. 2010, Jamieson 2015). The hydrostatic pressure is increasing linear with depth (1 atmosphere for every 10 m depth), representing a continuous gradient essentially influencing adaptions to the deep sea (Thistle 2003, Ramirez-Llodra et al. 2010, Jamieson 2015).

Unique habitats that are essentially differing to these common deep-sea habitats are chemosynthetic systems like hydrothermal vents and cold seeps. They are usually found along active mid-ocean ridges, continental margins and back-arc spreading centres (Van Dover 2002, Tunnicliffe et al. 2003, Govenar 2010, Ramirez-Llodra et al. 2010). The energy sources of these ecosystems are mainly influenced by chemical reactions of very hot (up to 407 °C) or cold fluids, originating from geological processes, with seawater. During these reactions, chemicals that are charged in the leaking fluids like sulphide, methane, hydrogen, manganese and different metals are creating a specific environmental habitat, where chemolitho-autotrophic microorganisms are assuming the role of in-situ primary producers for the specialized, associated fauna (e.g. Van Dover 2002, Tunnicliffe et al. 2003).

II. Diversity in the deep sea

The deep-sea benthos is generally distinguished in four major size classes: the megafauna are all animals large enough to be visible on the seabed, usually exceeding 1 cm (Gage and Tyler 1992), the macrofauna is compromising taxa with a body size from 250 – 500 µm up to around 1 cm, primarily found in the top 1 – 5 cm or at the sediment-water interface (Rex and Etter 2010), taxa belonging to the meiofauna are even smaller primary ranging from 32 – 1.000 µm and the microbiota is mainly represented by protists with a body size of only a few microns (Thistle 2003, Rex and Etter 2010). As the studies in this thesis are focused on the macrofauna, the following introduction and the general discussion is referring to this size class.

The benthic diversity in the deep sea is postulated to be remarkably high. It is comparable to the diversity found in shallow, warm, tropical communities (e.g. Hessler and Sanders 1967, Grassle 1989, Grassle and Maciolek 1992, Rex and Etter 2010). Many hypotheses about the high diversity in an environment that appears to be hostile and rather homogenous, have emerged since the first observations of the deep-sea macrofaunal species richness have been made (Sanders and Hessler 1969, Snelgrove and Smith 2002, Danovaro et al. 2009, McClain and Schlacher 2015). All estimates of diversity are still preliminary, as the deep sea is still the least explored ecosystem on earth and observations are mostly based on regional scales, even if sampling efforts have increased in the last decades,

(e.g. Ballard and Hively 2002, Danovaro et al. 2009, Ebbe et al. 2010, Rex and Etter 2010, Costello and Chaudhary 2017). One of the main diversity patterns found in the deep sea is the depth-diversity gradient, which means that diversity declines with depth, being highest in intermediate to bathyal depths and decreasing towards the abyss, often varying for different taxa and regions (e.g. Rex 1981, Rex et al. 1997, Levin and Gooday 2003, Rex and Etter 2010, Costello and Chaudhary 2017). It is widely accepted that this bathymetric pattern is primarily caused by energy limitation in the deep sea, as the input from sinking particulate organic carbon flux is decreasing exponentially with distance from the euphotic zones, like the surface water and the nutrient-rich coastal waters (Sibuet et al. 1989, Smith and Demopoulos 2003, Rex et al. 2006, Smith et al. 2008). Additionally, a reduction of the average organism size with increasing depth was found for the deep-sea benthos (Rex et al. 2006). Furthermore, a latitudinal gradient in deep-sea biodiversity was reported for various taxa (e.g. Rex et al. 1993, 2000, Lambshead et al. 2000). This pattern is still under debate (e.g. Ramirez-Llodra et al. 2010) and it rather seems that patterns of the global deep-sea diversity are much more complex and knowledge might be still too sparse, hence an ocean wide diversity model seems to be questionable (Rex and Etter 2010).

III. Distribution patterns in the deep sea

Distributional ranges are usually supposed to be broader for deep-sea species than their shallow-water counterparts (e.g. McClain and Hardy 2010, Higgs and Attrill 2015, Baco et al. 2016). The high dispersal potential in the deep sea is suggested to be related to the lack of perceived environmental variability, as variables like temperature, oxygen and salinity are almost constant over large distances in a connected habitat McClain and Hardy 2010). This general assumption is also often associated with the ability of many deep-sea species to distribute via planktonic larvae (e.g. Young et al. 1997, Young 2009). There is a correlation between the length of planktonic life stages and dispersal distance, but there are also many exceptions, highlighting the sparse knowledge about mechanisms and factors limiting or enhancing distribution patterns (Shanks 2009). Distribution ranges are also influenced by a combination of species-specific components, such as larval behaviour, buoyancy, mortality, developmental rates and physiological tolerances, which are almost always unknown for deep-sea species (Hilário et al. 2015).

The horizontal dispersal of planktonic larvae is linked to ocean currents and is mainly passive (Metaxas and Saunders 2009). It is supposed to be advantageous for planktonic larvae to stay in the deeper water currents even if higher currents

are usually stronger and could result in a transportation over large geographic distances over relatively short periods of time (Baco et al. 2016), but these fast currents can also lead to downstream advection of larvae, preventing the settlement in suitable regions (Byers and Pringle 2006: '…downstream is defined here as the direction of the mean current…'). Furthermore, vertical migration of larvae would require physiological tolerance for major changes in temperature and hydrostatic pressure, which are known to influence metabolic rates and vital processes of larvae significantly (Fiksen et al. 2007, Metaxas and Saunders 2009, Hilário et al. 2015). Moreover the constant low temperatures in the deep sea is influencing metabolic rates, hence prolonging larval duration and survival (O'Connor et al. 2007).

Another important factor, next to the mentioned species-specific components, influencing larval dispersal is topography. Geological features like ridges, seamounts and land masses have major influences on ocean currents, thus representing potential dispersal and distribution barriers (see McClain and Hardy 2010).

The Mid-Atlantic Ridge (MAR) is one of the most striking features, dividing the Atlantic abyssal longitudinal in an eastern and western basin, extending from Greenland to the Southern Ocean (Murray and Hjort 1912, Levin and Gooday 2003). The MAR is an underwater mountain chain with heights up to 3,000 m above the seafloor, restricting deep-water circulation between the two abyssal basins (Bower et al. 2002, Read et al. 2010, Shields and Blanco-Perez 2013). It is supposed that the MAR represents a physical barrier to abyssal species, as the vertical migration over the ridge would require a high physiological tolerance limit (Rex and Etter 2010, Etter et al. 2011, Shields and Blanco-Perez 2013). However, the MAR is interrupted by partially large ridge offsets, so called transform faults, caused by ongoing plate tectonic processes (Ball and Harrison 1970, Van Andel et al. 1971, Devey et al. 2018). These transform faults can extend off-axis for several hundreds of kilometres in fracture zones, influencing the circulation and mixing of water masses across the ocean basins (e.g. Polzin et al. 1996, Polzin 1997, Clément et al. 2017).

One of the largest transform faults, interrupting the MAR is the Vema Transform Fault (VTF) located in the tropical Atlantic (10° N), extending in the Vema-Fracture Zone (VFZ) roughly 300 km in east-west direction (Riehl et al. 2018a). The VFZ is known to be one of the major conduits through the MAR for water masses like the Antarctic Bottom Water (AABW), flowing from the western (Demerara Basin) to the eastern (Cape Verde Basin) Atlantic basins through this channel (e.g. Eittreim and Ewing 1975, McCartney et al. 1991, Mauritzen 2002). This pathway nature of the VFZ and its consequently potential influence on abyssal faunal exchange be-

tween the eastern and western Atlantic was one of the major research questions of the Vema-TRANSIT Expedition (bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study), which was conducted during winter 2014/2015 (Riehl et al. 2018a, Devey 2015). An east-west transect (~4,600 km) was sampled from the Cape Verde Basin, via the Demerara Basin towards the Puerto Rico Trench (PRT) to study, inter alia, the effect of the VFZ, as well as the depth transition of the hadal PRT for the dispersal of benthic invertebrates (Riehl et al. 2018a, Devey 2015). All presented research within this thesis is primarily based on the samples from the Vema-TRANSIT Expedition.

Cosmopolitan species (Hutchings and Kupriyanova 2018: '…usually assumes a very wide distribution, at least occurring in both major oceans basins (i.e. Pacific and Atlantic).') are still reported for many deep-sea groups like nematodes, foraminifera, molluscs, echinoderms and polychaetes (e.g. Tyler 1980, Gooday et al. 2004, Allen 2008, Vanreusel et al. 2010, Schüller and Hutchings 2012). Even though wide distribution ranges were shown for many taxa in the deep sea, modern research techniques like molecular tools and higher research efforts reveal a potential overestimation of wide-ranging and cosmopolitan species (e.g. McClain and Hardy 2010, Higgs and Attrill 2015, Hutchings and Kupriyanova 2018). One inherent bias is the taxonomic bias, which should be always taken into account. The correct identification of species is the basis for determining distribution ranges. Taxonomic bias can affect distribution ranges in opposite directions, an overestimation caused by missing species-specific characters and an underestimation caused by life history stages and phenotypic plasticity resulting in synonymous names (Vrijenhoek 2009). Furthermore, taxonomic bias can be even induced by different taxonomic approaches of different scientists (Paterson et al. 2009). Another problem is caused by cryptic species that are morphological indistinguishable, but genetically distinct (Bickford et al. 2007), which are found in a high degree in deep-sea species (Higgs and Attrill 2015). Cryptic species can occur sympatrically (e.g. Brasier et al. 2017), making the correct identification of species more complicated. Intensive revision of previously reported widespread species should be considered, including integrative taxonomic approaches, i.e. combination of molecular and morphological analyses, to realistically assess distribution ranges in the deep sea.

IV. Deep-sea polychaetes

Traditionally, the 'Polychaeta' and Clitellata were considered to form the phylum Annelida (segmented worms) (e.g. Fauchald 1977, Fauchald and Rouse

1997). After several analyses of morphological and molecular data of Annelida, 'Polychaeta' was found as paraphyletic with regards to groups like Clitellata, Echiura, Pogonophora and Sipunculida (e.g. Bleidorn et al. 2003, Struck et al. 2011, Weigert et al. 2014, 2016, Weigert and Bleidorn 2016). Despite the problematic phylogenetic status of 'Polychaeta', I will use the term polychaetes to refer to marine bristle worms throughout this thesis.

Polychaetes are found in all marine habitats from the intertidal down to the hadal trenches, in all latitudes and all size classes (e.g. Glasby et al. 2000, Díaz-Castañeda and Reish 2009, Jamieson 2015). In general, polychaetes consist of a presegmental 'head' (Prostomium) and a postsegmental (Pygidium) region, connected through chaeta bearing segmented trunk. This general morphological pattern exhibits a broad variety like different appendages (e.g. palps, tentacles, branchiae) and parapodia, reflecting the diverse lifestyle of polychaetes (e.g. Fauchald 1977, Hartmann-Schröder 1996, Glasby et al. 2000). Polychaetes can be found free-living (e.g. swimming and crawling), sessile (burrowed or tube dwelling) or even as commensals or parasites (Martin and Britayev 1998), showing many different feeding strategies (Jumars et al. 2015). Furthermore, the reproductive strategies of polychaetes include all types of reproduction (sexual and asexual) found within invertebrates, but many polychaete species bear planktonic larval stages (e.g. Wilson 1991, Glasby et al. 2000). The potential high diversity of marine polychaetes is also reflected by to date the high number of valid described species (Pamungkas et al. 2019: 11,456 species, 1,417 genera, 85 families).

Polychaetes are commonly found as one of the dominant groups with high abundances in the deep-sea benthic macrofauna (e.g. Fauchald and Jumars 1979, Grassle and Maciolek 1992, Herring 2002, Brandt et al. 2007, Fiege et al. 2010). They are supposed to play a major role in different deep-sea environments. Especially in the soft-sediments typical for the deep sea, as polychaetes are influencing crucial sediment parameters (e.g. porosity, particle sizes, fluxes) and the bioturbation through different feeding modes, tube building and burrowing (Snelgrove 1997). Another important role they play is in recolonization disturbed habitats, as polychaetes are often found as pioneer species after pollution or disturbance events (Grassle and Morse-Porteous 1987, Glover et al. 2001, Schüller and Ebbe 2007, Díaz-Castañeda and Reish 2009). The ability to settle in disturbed habitats is often associated with an ecological flexibility and opportunistic widespread polychaete species are commonly reported first in such areas (Glover et al. 2001, Norkko et al. 2006, Schüller and Ebbe 2007, Díaz-Castañeda and Reish 2009, Chapter 3).

The partially enormous dispersal potential of some polychaete species are pro-

posed to be linked to their tendency for developmental dispersal via planktonic larvae ((e.g. Young et al. 1997, McClain and Hardy 2010, Yearsley and Sigwart 2011).

It was assumed for a long time that polychaetes have unusually widespread or cosmopolitan distributions compared to other invertebrates, resulting in many records of cosmopolitan distributed species (reviewed in Hutchings and Kupriyanova 2018). Yet, this large proportion of reported widespread polychaete species is under debate (e.g. Nygren 2014, Hutchings and Kupriyanova 2018). Even though, the potential for wide geographic ranges, especially for deep-sea polychaetes had not been rejected, a large amount of reported widespread species had to be revised. For instance, Terebellides stroemii Sars, 1853 was considered to have a cosmopolitan distribution, but several detailed morphological studies revealed distinct species, partially with very narrow distribution ranges (Hutchings and Peart 2000, Parapar and Hutchings 2015, Nygren et al. 2018). Another example is the formerly cosmopolitan Spiophanes bombyx (Claparéde, 1870), whose type locality is the Gulf of Neaples, Italy. This species was also reported from different oceans (e.g. North Atlantic, North Pacific Ocean, NW Africa and Chile) with slight intraspecific variations, which were found to indicate a species complex and molecular analyses revealed several cryptic species (Meißner and Blank 2009). There are many other examples for widespread polychaetes that have been found to consist of different species with much more restricted distribution ranges (reviewed in Nygren 2014, Hutchings and Kupriyanova 2018). Hence, even if real cosmopolitan polychaetes seem to exist (e.g. Schüller and Hutchings 2012, Georgieva et al. 2015), widespread or cosmopolitan reported species should be always treated with caution and questioned.

Because polychaetes show competences for wide distribution ranges and usually occur in high abundance, they represent a suitable model taxon for examining diversity and distribution patterns in the deep sea.

Within this thesis, species of two polychaete families, Spionidae and Polynoidae, were studied in detail. Spionidae are usually found in high abundances in deep-sea samples in a large variety of habitats (e.g. Maciolek 1981a, Glover et al. 2001, Hilbig and Blake 2006, Fiege et al. 2010). Spionids are characterized by grooved feeding palps, used for suspension and deposit feeding, as well as for collecting particles for tube building (e.g. Jumars et al. 2015, Blake et al. 2018). Furthermore, spionids are supposed to be successful in distribution and adaption to different habitats because of their flexibility in feeding behaviour and plasticity in reproduction and development (Blake et al. 2018). In spionids, all types of invertebrate reproduction and feeding modes are represented and they are even

able to switch from deposit to suspension feeding with changing conditions (Glasby et al. 2000, Jumars et al. 2015). The more detailed studied Laonice, Prionospio and Aurospio are often the most common spionid genera in the deep-sea, but still the knowledge about the biology and systematics of deep-sea spionids is very limited (e.g. Glasby et al. 2000, Blake et al. 2018, Bogantes et al. 2018).

Like spionids, Polynoidae are found in all marine habitats, but there are 13 subfamilies that seem to occur exclusively in the deep sea (see Bonifácio and Menot 2019). Polynoids are characterized by a dorsum covered with scales. With some commensal exceptions, they are free living and mobile (crawling or even swimming) carnivores (Glasby et al. 2000, Jumars et al. 2015). Although, polynoids are one of the most diverse polychaete families and widely distributed, they are often absent or rare in deep-sea samples, which is supposed to be linked to their mobility, enabling them to avoid sampling gears (Bonifácio and Menot 2019).

Both families strongly differ in their adult lifestyle, as polynoids are free living, mobile and carnivorous, whereas spionids (the herein studied genera) are sessile, tube living and suspension or deposit feeders (Jumars et al. 2015). Nonetheless, both, Spionida and Polynoidae, are known to have planktonic larval stages, resulting in high dispersal potential (e.g. Glasby et al. 2000, Neal et al. 2014, Blake et al. 2018), making them ideal taxa for the study of distribution ranges in the deep sea.

V. Challenges in the identification of deep-sea polychaetes

The adequate identification of species is a crucial basis for interpreting results of deep-sea studies (e.g. studies on diversity, distribution, general mechanisms). As already mentioned (Section III) cryptic species and taxonomic bias are occurring repeatedly, potentially resulting in wrong conclusions.

Taxonomic work with deep-sea polychaetes is additionally challenging, as they are soft-bodied animals, vulnerable to damages during sampling procedures (Paterson et al. 2009, Nygren 2014, Chapter 4, 5 and 6). Their sensitivity often cause fragmentation or/and the loss of appendages, resulting in the lack of important species discriminating morphological characters. A current approach for the identification of species is the combination of molecular and morphological analyses, using integrative taxonomy (Will et al. 2005, Wheeler 2018) in an evolutionary systematic context (Glaubrecht 2007, 2010). "…Evolutionary systematics comprises the study of taxonomic diversity, disparity and genetic variability and of the underlying evolutionary causes of speciation on the basis of phylogenetic systematics..." (Schwentner et al. 2014). Extreme-

ly carefully handling of deep-sea samples during sieving, as well as appropriate fixation (e.g. anaesthetizing before fixation) should be obviously integrated in sampling procedures (e.g. Glover et al. 2015, Chapter 4, 5 and 6).

Within this thesis the discrepancy between species identification based solely on morphology and species delimitation with molecular analyses was observed (Chapter 4, 5 and 6), supporting the importance of integrative taxonomy to avoid incorrect interpretations of patterns in the deep sea.

VI. Aims and hypotheses

Despite many hypotheses proposed for diversity and distribution patterns of benthic invertebrates in the deep sea (e.g. McClain and Hardy 2010, Rex and Etter 2010, McClain and Schlacher 2015), there is a general consensus regarding the importance of species-specific factors influencing these patterns.

Based on the still sparse knowledge about diversity and distribution ranges in the deep sea the results presented in this thesis were conducted to expand this knowledge. Therefore the diversity and distribution patterns of polychaetes and selected spionid and polynoid genera from the tropical Atlantic were investigated. Both families were proposed to have wide dispersal potential via planktonic larval stages. A connection of the eastern and western abyssal through the VFZ is tested, as well as the general horizontal and vertical distribution ranges. Specimens from the abyssal tropical Atlantic, the hadal PRT and other oceanic areas like the Pacific were compared and analysed for Laonice, Prionospio, Aurospio and Bathypolaria.

The following hypotheses will be discussed:

- Abundance is decreasing seawards with distance from continental slopes
- Diversity of deep-sea polychaetes is increasing with habitat heterogeneity and increasing food input
- The diversity in hadal depths is lower compared to abyssal depths
- Rare species have restricted distribution ranges, whereas species with high abundances are widespread
- The VFZ is a potential connection for the distribution of polychaete species across the MAR
- Hadal species are most likely restricted to these depths or/and originating in the surrounding abyssal

- Cosmopolitan distribution is existing in deep-sea polychaetes

VII. Summary

The main focus of the thesis is about polychaetes from the Vema-Fracture Zone (VFZ) and the Puerto Rico Trench (PRT).

The general macrofaunal composition in this area is analysed in Chapter 2. Diversity and distribution of all polychaete families, as well as spionid and polynoid species along the VFZ were investigated with classical morphology, to test a connection between the eastern and western abyssal across the Mid-Atlantic Ridge (Chapter 3). Additionally, three spionid genera (Chapter 4 and 5) and one polynoid genus (Chapter 6) were analysed with molecular methods.

Next to the diversity and distribution ranges of species in the tropical Atlantic and discrepancies between morphological and molecular delimitated species, the spionid genus Laonice was analysed with available data from other oceanic areas (Chapter 4). Comparable studies were conducted with Prionospio and Aurospio species, but a potential pan-oceanic distribution was tested with a large dataset from Prionospio and Aurospio specimens from the central Pacific (Chapter 5).

The last chapter is dealing with the diversity and distribution of the hitherto monotypic genus Bathypolaria, whereby based on the high abundance of this polynoid genus in the hadal PRT the vertical dispersal potential was additionally studied (Chapter 6).

CHAPTER 2

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

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

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ABSTRACT

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

The composition of the macrofauna from the epibenthic sledge catches yielded a total of 21,332 invertebrates. Crustacea occurred most frequently (59%) with 12,538 individuals followed by Annelida (mostly Polychaeta) (26%) with 5491 individuals, Mollusca (7%) with 1458 individuals, Echinodermata (4%) with 778 individuals, Nematoda (2%) with 502 individuals and Chaetognatha (1%) with 152 and Porifera (1%) with 131 individuals. All other taxa occurred with overall less than ten individuals (Hemichordata, Phoronida, Priapulida, Brachiopoda, invertebrate Chordata, Echiurida, Foraminifera (here refereed to macrofaunal Komokiacea only), Chelicerata, Platyhelminthes). Within the Crustacea, Peracarida (62.6%) with 7848 individuals and Copepoda (36.1%) with 44,526 individuals were the most abundant taxa. Along the abyssal Vema-Fracture Zone macrofaunal abundances (ind./1000 m^2) were generally higher on the eastern side, while the highest normalized abundance value was reported in the Puerto Rico Trench at abyssal station 14-1 2313 individuals/1000 m^2. The lowest abundance was reported at station 11-4 with 120 ind./1000 m^2 located at the western side of the Vema-Fracture Zone. The number of major macrofaunal taxa (phylum, class) ranged between five (stations 12-5, 13-4 and 13-5 at hadal depths in the Puerto Rico Trench) and 14 (station 9-8) in the western abyssal basin of the Vema-Fracture Zone. Differences are seen in the distribution of Porifera at macrofaunal level between eastern and western sides of the Vema-Fracture Zone. Macrofaunal composition of the study area is compared with data from other expeditions in the Atlantic and the northwest Pacific Ocean.

1. Introduction

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

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communities are tectonic processes, but it is unknown to which extent and how it determines the distribution of benthic species.

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

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

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

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

2. Material and methods

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

2.1. Study area

Sampling was performed along the VFZ and the Vema Transform Fault (VTF) in the tropical North Atlantic (Devey et al., 2015). Five sites were sampled respectively in the eastern and western VFZ and one station within the VTF (Table 1 and Fig. 1). The VFZ and VTF are roughly located at latitude 11° N (exact station locations are provided in Table 1). It is part of a group of transform faults which offsets the Mid-Atlantic Ridge by 320 km (Louden et al., 1986; Cannat et al., 1991). It is composed of a flat transform valley bounded by steep walls with some peaks reaching as high as 500 m below surface (Morozov et al., 2010). Both, the VFZ and VTF are strongly affected by the advection of the Antarctic Bottom Water, which flows into the VTF from the western side. This Antarctic water mass flows below 4300 m and is characterized by low temperature, low salinity, and high nutrient content if compared to the overlaying North Atlantic Deep Water (Morozov et al., 2010, 2015). The physical environment of the VFZ including the bathymetry is described in detail by Devey et al. (In this issue). The general hydrography of the northern North Atlantic (Schäfer et al., 2001) and South Atlantic (Wefer et al., 1996) is published in two books.

2.2. Deployment of C-EBS

A camera-epibenthic sledge (C-EBS) designed for sampling small epi- and suprabenthic macrofauna (from half a millimetre to centimetres of size) at any depth and on any substrate was used (Brandt et al., 2013). The C-EBS was equipped with supra- and epibenthic samplers possessing two plankton nets (500 µm) with cod ends (300 µm) placed in temperature-isolated thermo-boxes for work in tropical waters, but keeping the animals in cold bottom water for later studies including molecular genetics. An opening-closing mechanism, active at bottom contact, prevented captures of pelagic fauna. The haul distances were calculated using the time and the speed (ships speed with 1 knot, and winch speed with −0.5 m/sec. (equals one knot)) (as outlined in Anon, 2015) until the C-EBS left the ground, which was indicated by the tension meter. At station 9-2 on the western side of the VFZ the C-EBS got stuck and remained on the ground for almost three hours until it was possible to retrieve it back on the vessel and trawling time could not be determined. In this case, the haul length was calculated by means of a TSK flowmeter placed in the upper net, even though this could be affected by bottom currents. Trawled distances were used to calculate the area sampled by the sledge (1 m width, see Brenke, 2005). To allow the comparison between stations, data were standardized to 1000 m^2.

Additionally, the C-EBS carries an autonomous digital underwater video camcorder and a still camera, both equipped with the required energy and control units as well as a Seaguard RCM DW for measuring data on temperature (°C), pressure (hPa), conductivity (mS/cm), current velocity (m/s) and oxygen (µM) concentration when the sledge is on ground. As these electronic devices can only be deployed until 6000 m depth, they were not deployed at hadal depths in the Puerto Rico Trench.

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

2.3. Sample treatment and comparability

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

For comparison between stations, abundance data were expressed as individuals per 1000 m^2 trawled distances.

2.4. Statistics

Datasets comparable to the one presented here were available from previous expeditions that used similar sampling protocols, e.g. to the South Polar Front, the Scotia Arc area and Subantarctic, the Cape, Angola, Guinea, Argentinian and Brazilian basins and in the NW Pacific the Sea of Japan and the Kuril-Kamchatka abyssal plain either as published data (Brandt et al., 2013, 2015) or from the Forschunginstitut Senckenberg, Deutsches Zentrum für Marine Biodiverstätsforschung and British Antarctic Survey expedition databases (unpublished data). PRIMER v6 (Clarke and Gorley, 2006) was used to compare the macrofaunal assemblages of each of the Vema-TRANSIT stations, between Vema-TRANSIT and previous expeditions, as well as abyssal assemblages separately. The Bray-Curtis similarity coefficient is applied to standardized abundance data of all macrofaunal taxa present in the EBS samplers obtaining a similarity matrix (Clarke and Gorley, 2006). Hierarchical clustering with group-averaged linking and non-metric multidimensional scaling (nMDS) was then performed using these matrixes. One-way ANOSIM tests were performed (Vema-Transit, global

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

SO237	Sation	Area	Date	off Deck	Start Ship Position	Start Ship Position	End Ship Position	End Ship Position	Depth max	Towing Distance	O^2 Bottom	Temp Bottom	Bottom Current
			UTC	UTC	Lon [°W]	Lat [°N]	Lon [°W]	Lat [°N]	[m]	$Distance_{TRW-W}$ F = Floweter	[µM]	[°C]	[cm/s]
	Station	Area	Date	Hour[a]	Coordinates				Depth max.	Towing distance[b]	O_2	Temp	Current
					start ship position		end ship position		[m]	[m]	[µM]	[°C]	[cm/s]
EBS 1	2-6	E VFZ	20–12–14	07:52	10° 43.17' N	25° 04.49' W	10° 43.80' N	25° 03.73' W	5520	1846	237.5	2.30	1.7
EBS 2	2-7	E VFZ	20–12–14	16:30	10° 42.06' N	25° 04.26' W	10° 42.94' N	25° 03.16' W	5507	2020	238.2	2.29	1.1
EBS 3	4-8	E VFZ	26–12–14	21:59	10° 24.96' N	31° 05.19' W	10° 25.63' N	31° 04.38' W	5725	1750	238.3	2.31	6.6
EBS 4	4-9	E VFZ	27–12–14	06:55	10° 24.94' N	31° 03.83' W	10° 25.67' N	31° 02.98' W	5733	1900	238.0	2.31	2.0
EBS 5	6-7	E VFZ	02–01–15	14:38	10° 21.33' N	36° 55.93' W	10° 21.84' N	36° 55.06' W	5079	1980	245.8	2.29	2.4
EBS 6	6-8	E VFZ	02–01–15	23:12	10° 22.25' N	36° 56.05' W	10° 22.66' N	36° 55.35' W	5127	1400	245.4	2.21	2.1
EBS 7	8-4	MAR	06–01–15	15:45	10° 43.00' N	42° 40.67' W	10° 43.01' N	42° 39.73' W	5178	1750	239.1	1.81	2.6
EBS 8	9-2	W VFZ	11–01–15	07:41	11° 40.58' N	47° 58.93' W	11° 40.45' N	47° 59.00' W	4986	673[c]	240.9	1.79	6.1
EBS 9	9-8	W VFZ	12–01–15	15:12	11° 39.21' N	47° 54.96' W	11° 39.37' N	47° 53.98' W	5001	1613	241.6	1.80	2.2
EBS 10	11-1	W VFZ	14–01–15	06:16	12° 05.76' N	50° 28.85' W	12° 05.81' N	50° 27.96' W	5088	1320	239.2	1.76	4.9
EBS 11	11-4	W VFZ	14–01–15	15:08	12° 04.76' N	50° 28.94' W	12° 04.83' N	50° 28.14' W	5108	1416	239.4	1.76	2.6
EBS 12	12-5	PRT	20–01–15	19:56	19° 46.50' N	66° 50.97' W	19° 46.85' N	66° 49.99' W	8338	1611	–	–	–
EBS 13	12-6	PRT	21–01–15	03:26	19° 48.49' N	66° 45.44' W	19° 48.61' N	66° 45.11' W	8336	602	–	–	–
EBS 14	13-4	PRT	23–01–15	03:00	19° 46.73' N	67° 06.21' W	19° 47.13' N	67° 05.79' W	8317	750	–	–	–
EBS 15	13-5	PRT	23–01–15	12:05	19° 49.85' N	67° 02.91' W	19° 50.14' N	67° 02.60' W	8042	840	–	–	–
EBS 16	14-1	PRT	24–01–15	16:35	19° 01.63' N	67° 09.73' W	19° 02.11' N	67° 09.43' W	4552	764	261.1	2.25	5.3
EBS 17	14-2	PRT	24–01–15	22:23	19° 04.16' N	67° 08.11' W	19° 04.67' N	67° 07.75' W	4925	968	257.7	2.24	2.1

multi-expedition and global abyssal only multi-expedition) in order to investigate the differences between groups of stations. Depth zones are defined as Southern Ocean shelf (200 m–< 1000 m depth), bathyal (200 m–< 3000 m depth), abyssal (3000 m–< 6000 m depth), and hadal (> 6000 m depth). Areas are defined as Puerto Rico trench (PRT), south Atlantic (S_Atl), southeast Atlantic (SE_Atl), southwest Atlantic (SW_Atl), Southern Ocean (SO), northwest Pacific (NW_Pac), Vema Fracture Zone (VFZ). Regions are defined as Aghulas Basin, Angola Basin, Argentine Basin, Brazil Basin, Cape Basin.

2.5. Terminology

We use the term "common" if we talk about a number of individuals per station of ~100, with the term "rare" we refer to singletons, doubletons or <10 individuals per species in each whole sample. The word "taxa" is used for the main sorted groups of invertebrates of different taxonomic ranks (phylum, class). Abundance refers to standardized values (ind./1000 m^2).

3. Results

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

3.1. C-EBS deployment

The C-EBS was deployed with camera systems and CTD along the VFZ. The towing distance ranged between 602 and 2020 m (Table 1). The oxygen concentration varied from 237.51 µM on the eastern side of the VFZ to 261.13 µM at the abyssal station in the PRT. The bottom

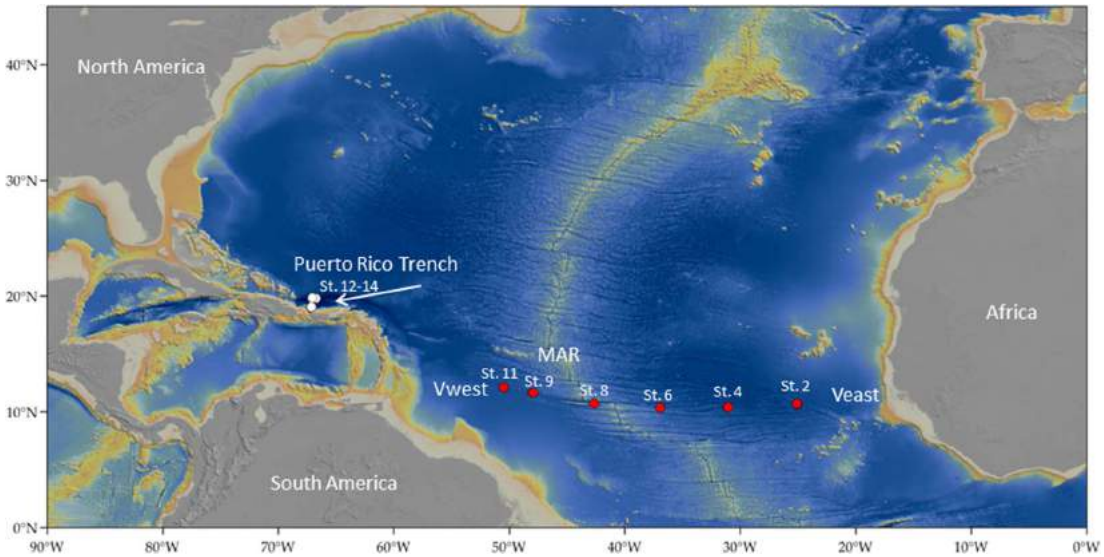

Fig. 1. Sites sampled across the Vema-Fracture Zone and in the Puerto Rico Trench (Map: courtesy of Nico Augustin).

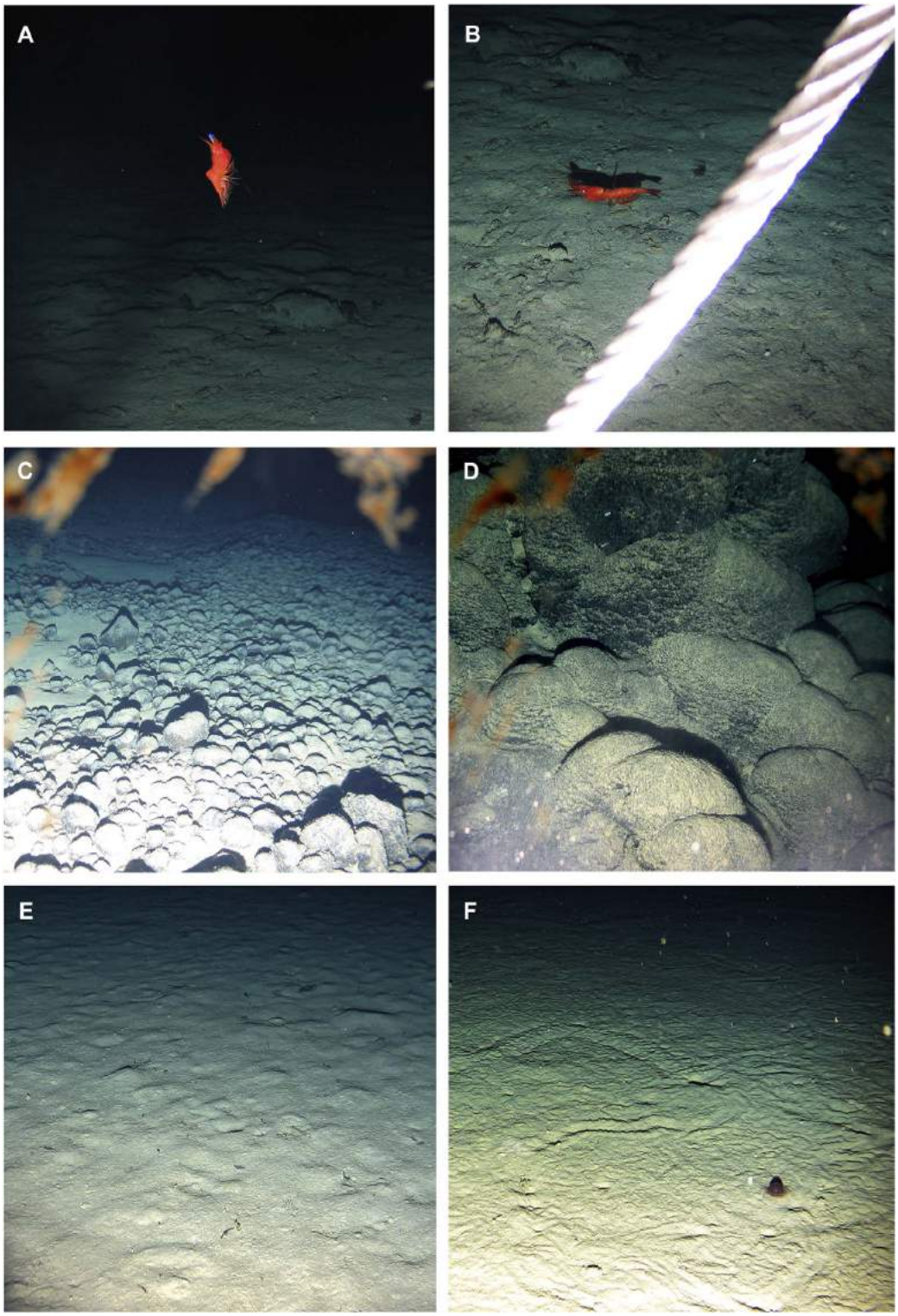

Fig. 2. A, Deep sea prawn (indet. sp. 1) with remarkably blue scaphocerites; station 9-2, 4986 m (VFZ); B, Deep sea prawn (cf. *Benthesicmus* sp. 1); station 9-2 (VFZ), 4986 m (the towing wire is visible in front); C, Field of polymetallic nodules; station 9-2 (VFZ), 4986 m; D, Rock formation build of pillow lava presumably covered with Ferro-manganese crusts; station 9-2 (VFZ), 4986 m; E, Sediment surface with small pieces of *Sargassum* (Phaeophyceae; brown macroalgae); station 14-1 (PRT), 4552 m; F, Sediment surface with many traces of life (presumably from holothurians) and a planktonic Hydromedusa float over the sediment, station 4-9 (VFZ), 5733 m.

water temperature showed an influence of the Antarctic bottom water on the western side of the VFZ where the water was slightly colder with 1.76 °C (station 11-4) compared to the MAR (station 8-4) with 1.81 °C and the eastern side of the VFZ with more than 2 °C, for example 2.313 °C at station 4–8. The bottom current velocities varied between 1.1 cm/s (station 2–7) and 6.58 cm/s (station 4–8) on the eastern side

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

	Area	Eastern VFZ						MAR	Western VFZ				PRT						
	Stations	2-6	2-7	4-8	4-9	6-7	6-8	8-4	9-2	9-8	11-1	11-4	12-5	12-6	13-4	13-5	14-1	14-2	
Taxa	Depth (m)	5520	5507	5725	5733	5079	5127	5178	4986	5001	5088	5108	8338	8336	8317	8042	4552	4925	Total
Annelida		275	804	697	977	376	607	391	24	206	59	51	48	84	36	40	374	442	5491
Brachiopoda		–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	2
Bryozoa		–	–	–	–	6	1	–	–	6	5	–	–	–	–	–	–	–	18
Chaetognatha		4	28	31	18	9	15	15	2	6	7	–	2	–	4	–	3	8	152
Chelicerata		–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Chordata		–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	2
Cnidaria		–	14	6	2	4	30	7	–	4	4	3	–	–	–	–	1	3	78
Crustacea		586	1543	1752	1793	930	1058	725	83	559	100	80	406	275	313	247	1216	872	12538
Echinodermata		12	62	226	236	10	13	8	–	31	–	2	42	20	12	4	45	55	778
Echiura		–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2
Foraminifera		–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	2
Hemichordata		1	4	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	7
Mollusca		22	159	268	220	96	135	81	8	48	17	20	64	19	52	27	105	117	1458
Nematoda		16	130	29	63	26	119	20	4	28	8	1	0	1	0	1	14	42	502
Nemertea		1	6	2	1	10	8	–	1	4	1	–	–	1	–	–	–	–	35
Phoronida		–	2	–	–	–	2	–	–	–	–	–	–	–	–	–	2	1	7
Platyhelminthes		2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Porifera		6	9	4	1	4	3	1	8	49	6	8	–	2	–	–	6	24	131
Priapulida		–	5	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	7
Sipunculida		2	13	2	6	18	24	8	2	21	5	5	–	–	–	–	–	2	108
Indet.		1	4	–	–	–	–	1	4	–	1	–	–	–	–	–	–	–	11
	Total	928	2783	3018	3318	1489	2016	1258	139	965	214	170	562	403	417	319	1767	1566	21332

of the VFZ, 2.60 cm/s at the MAR (station 8-4) and between 2.58 cm/s (station 11-4) and 6.11 cm/s (station 9-2) on the western side of the VFZ. At the abyssal station 14-1 in the PRT the current velocity was 5.24 cm/s (Table 1).

The camera system did not work properly at all stations. Some sample pictures are presented in Fig. 2 showing the seafloor at station 9-2 on the western side of the VFZ when the C-EBS landed on the seafloor (Fig. 2A, B) and the field of manganese nodules and rocks shortly before the EBS got stuck at this station (Fig. 2C, D). The abyssal plain of the PRT was characterized by an even and flat topography with few shallow mounds and depressions (Fig. 2E), while the eastern side of the VFZ (station 4–9) showed a number of "Lebensspuren" and a small hydromedusa (Fig. 2F).

3.2. Faunistic composition

In total, 21,332 benthic macrofaunal invertebrate specimens were collected from the C-EBS (Table 2). Crustacea, Annelida and Mollusca occurred at all stations. Crustacea was the most abundant group in the material with 12,538 specimens (58,8%) followed by Annelida (mostly Polychaeta) with 5491 specimens (25,7%), Mollusca with 1458 specimens (6,8%), and Echinodermata with 778 specimens 3,6%), while Nematoda (502 specs. 2,4%), Chaetognatha (152 specs, 0,7%) and Porifera (131 specs, 0,6%) were less frequent. Rare taxa which occurred with less than ten individuals in the samples (< 0.1%) were Hemichordata, Phoronida, Priapulida, Brachiopoda, Chordata (2 appendicularian larvae), Echiurida, Komikiacea, Chelicerata and Platyhelmintes (Fig. 3).

For comparability of abundances between stations, data of the taxa were normalized to 1000 m trawled distances per station (Table 3) (Fig. 4A, B). Within the Crustacea, Peracarida with 7848 individuals and Copepoda (Harpacticoida and Calanoida) with 4526 individuals were dominating (Table 4). Ostracoda occurred with 145 individuals and were most prevalent on the eastern side of the VFZ, as were Eucarida which only occurred with 17 individuals). Only 1 specimen of Cirripedia was sampled at station 11-1 in the western abyssal basin of the VFZ.

Between the C-EBS stations, total abundances varied from 120 to 2312 individuals/1000 m^2 (Table 3, Fig. 4A, B). The lowest number of

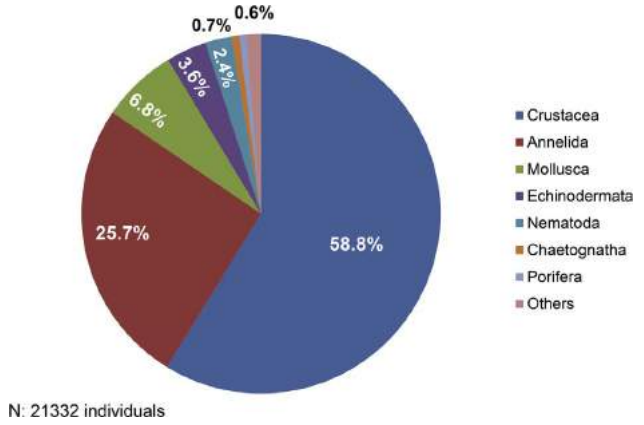

Fig. 3. Global composition of the macrofauna sampled by means of a C-EBS during the Vema-TRANSIT expedition. Others: taxa which contribute with less than 0.5% to the total individuals; i.e. Sipunculida, Cnidaria, Nemertea, Bryozoa, Priapulida, Phoronida, Hemichordata, Plathyelmintha, Brachiopoda, Chordata,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

invertebrates was reported at station 11-4 with 120 individuals/1000 m^2 at the western side of the VFZ. In the PRT we found the highest number of invertebrates at station 14-1 with 2313 individuals/1000 m^2 at 4552 m depth. The number of invertebrate taxa ranged between five (stations 12-5, 13-4, and 13-5 at hadal depths) and 14 (station 9-8) in the western abyssal basin of the VFZ (Fig. 4C).

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

Table 3
Abundance data (individuals/1000 m^2) of macrofauna of the Vema-TRANSIT stations.

	Area	Eastern VFZ						MAR	Western VFZ				PRT					
	Stations	2-6	2-7	4-8	4-9	6-7	6-8	8-4	9-2	9-8	11-1	11-4	12-5	12-6	13-4	13-5	14-1	14-2
Taxa	Depth (m)	5520	5507	5725	5733	5079	5127	5178	4986	5001	5088	5108	8338	8336	8317	8042	4552	4925
Annelida		149.0	398.0	398.3	514.2	189.9	433.6	223.4	30.5	127.7	44.7	36.0	29.8	139.5	48.0	47.6	489.5	456.6
Brachiopoda		–	–	–	–	–	–	–	1.3	0.6	–	–	–	–	–	–	–	–
Bryozoa		–	–	–	–	3.0	0.7	–	–	3.7	3.8	–	–	–	–	–	–	–
Chaetognatha		2.2	13.9	17.7	9.5	4.5	10.7	8.6	2.5	3.7	5.3	–	1.2	–	5.3	–	3.9	8.3
Chelicerata		–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–
Chordata		–	–	–	0.5	–	–	–	–	–	0.8	–	–	–	–	–	–	–
Cnidaria		–	6.9	3.4	1.1	2.0	21.4	4.0	–	2.5	3.0	2.1	–	–	–	–	1.3	3.1
Crustacea		317.4	763.9	1001.1	943.7	469.7	755.7	414.3	105.6	346.6	75.8	56.5	252.0	456.8	417.3	294.0	1591.6	900.8
Echinodermata		6.5	30.7	129.1	124.2	5.1	9.3	4.6	–	19.2	–	1.4	26.1	33.2	16.0	4.8	58.9	56.8
Echiura		–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	1.3	–
Foraminifera		–	–	–	–	–	0.7	–	1.3	–	–	–	–	–	–	–	–	–
Hemichordata		0.5	2.0	–	–	–	–	0.6	–	–	–	–	–	1.7	–	–	–	–
Mollusca		11.9	78.7	153.1	115.8	48.5	96.4	46.3	10.2	29.8	12.9	14.1	39.7	31.6	69.3	32.1	137.4	120.9
Nematoda		8.7	64.4	16.6	33.2	13.1	85.0	11.4	5.1	17.4	6.1	0.7	–	1.7	–	1.2	18.3	43.4
Nemertea		0.5	3.0	1.1	0.5	5.1	5.7	–	1.3	2.5	0.8	–	–	1.7	–	–	–	–
Phoronida		–	1.0	–	–	–	1.4	–	–	–	–	–	–	–	–	–	2.6	1.0
Platyhelminthes		1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Porifera		3.3	4.5	2.3	0.5	2.0	2.1	0.6	10.2	30.4	4.5	5.6	–	3.3	–	–	7.9	24.8
Priapulida		–	2.5	–	–	–	–	–	1.3	0.6	–	–	–	–	–	–	–	–
Sipunculida		1.1	6.4	1.1	3.2	9.1	17.1	4.6	2.5	13.0	3.8	3.5	–	–	–	–	–	2.1
Indet.		0.5	2.0	–	–	–	–	0.6	5.1	–	0.8	–	–	–	–	–	–	–
	Total	502.7	1377.9	1724.4	1746.4	752.0	1439.8	719.0	176.9	598.3	162.3	119.9	348.8	669.5	555.9	379.7	2312.7	1617.8

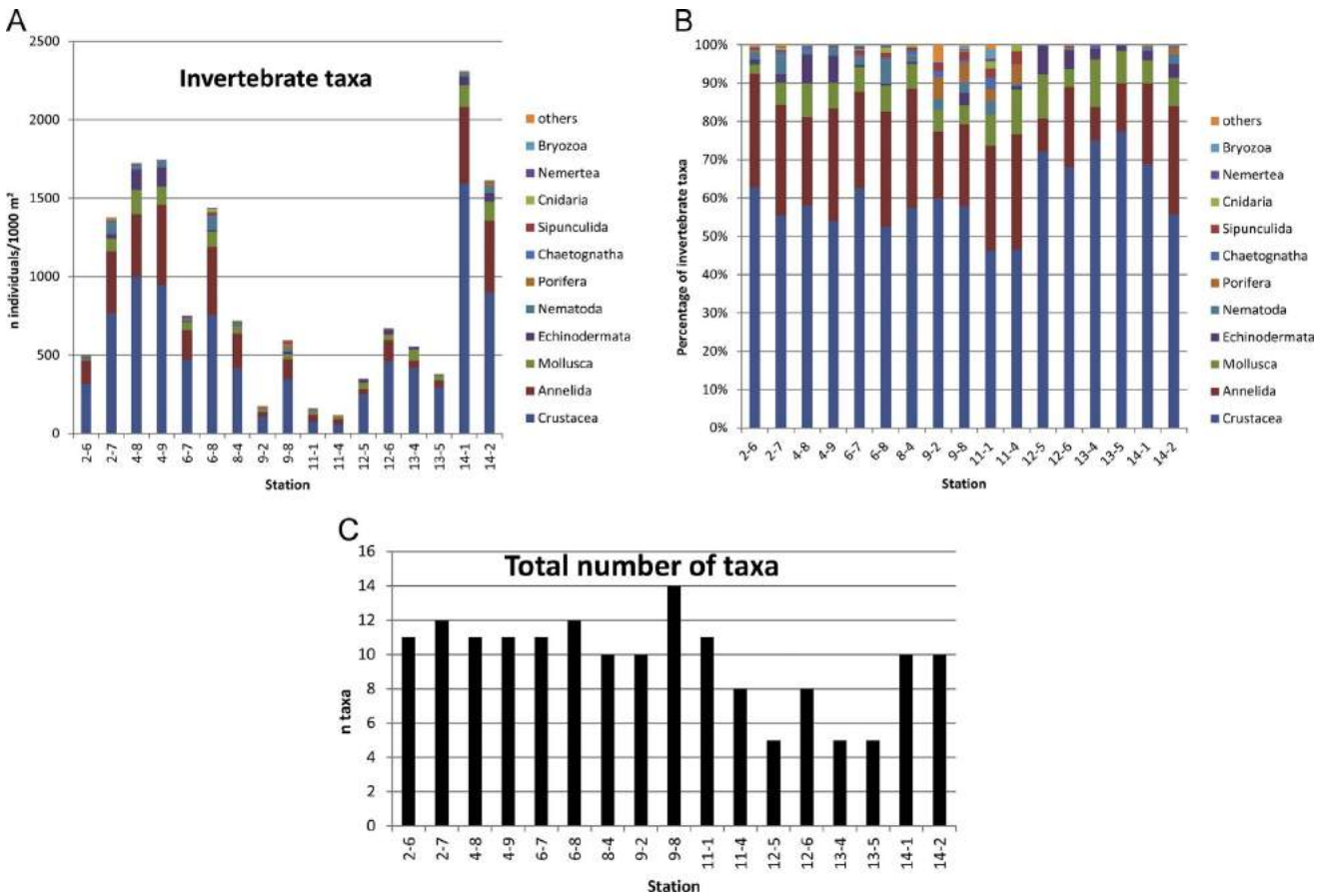

Fig. 4. A: Abundance (ind./1000 m2) of macrofauna sampled by means of a C-EBS at each station during the Vema-TRANSIT expedition. Others = taxa occurring with less than 10 individuals in the samples (Hemichordata, Phoronida, Priapulida, Brachiopoda, Chordata, Echiurida, Foraminifera, Cheliceratаа, Plathelminthes,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

Table 4
Crustacea of the Vema-TRANSIT stations.

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

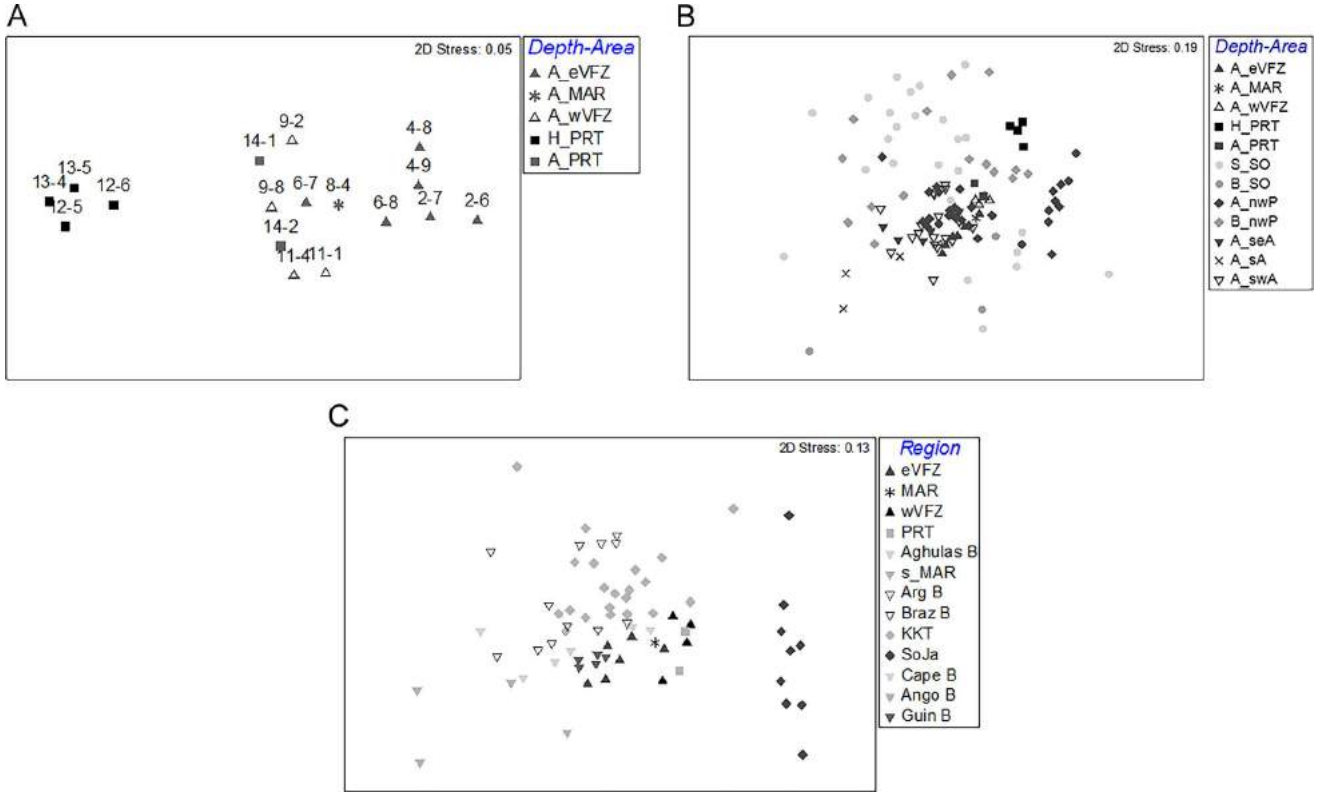

Fig. 5. A: MDS of standardized Bray-Curtis similarities from VEMA TRANSIT datasets (for abbreviations see 2.6). Abbreviations: A_eVFZ – Abyssal eastern basin Vema-Fracture Zone, A_MAR – Abyssal Mid-Atlantic Ridge, A_nwP – Abyssal northwestern Pacific, A_PRT – Abyssal Puerto Rico Trench, A_wVFZ – Abyssal western basin Vema-Fracture Zone. B: nMDS of standardized Bray-Curtis similarities from multiple EBS macrofauna datasets (for abbreviations see 2.6). Abbreviations: A_eVFZ – Abyssal eastern basin Vema-Fracture Zone, A_MAR – Abyssal Mid-Atlantic Ridge, A_nwP – Abyssal northwestern Pacific, A_PRT – Abyssal Puerto Rico Trench, A_sA – Abyssal southern Atlantic, A_seA – Abyssal southeastern Atlantic, A_swA – Abyssal southwestern Atlantic, A_wVFZ – Abyssal western basin Vema-Fracture Zone, B_nwP – Bathyal northwestern Pacific, B_SO – Bathyal Southern Ocean, H_PRT – Hadal Puerto Rico Trench, S_SO – Shelf Southern Ocean. C: nMDS of standardized Bray-Curtis similarities from multiple abyssal EBS macrofauna datasets (for abbreviations see 2.6). Abbreviations: Aghulas B – Aghulas Basin, Ango B – Angolas Basin, Arg B – Argentine Basin, Braz B – Brazilian Basin, Cape B – Cape Basin, eVFZ – eastern basin Vema-Fracture Zone, Guin B – Guinea Basin, KKT – Kurielen Kamchatka Trench, MAR –Mid-Atlantic Ridge, PRT –Puerto Rico Trench, sMAR – southern Mid Atlantic Ridge, SoJa – Sea of Japan, wVFZ – western basin Vema-Fracture Zone.

are still higher than those of the abyssal VFZ in the western basin.

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

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

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

4. Discussion

4.1. C-EBS deployment

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

Sediments at abyssal depths of around 5000 m were fine and silty (Devey et al., In this issue, Linse et al., In this issue), especially at the eastern side of the VFZ, what was possibly a reason why we found more crustaceans here compared to the western side of the VFZ. The benthic habitats in the east did not contain manganese nodules, while the habitats sampled in the West contained a huge number of nodules or manganese crust (Fig. 2C, D). Furthermore, the temperature differed along the VFZ. It was colder on the western side of the VFZ than on the eastern side, indicating an influence of the cold Antarctic bottom water extending north (e.g. Rintoul et al., 2001, 2012; Reid, 1996) and possibly causing faunal similarities between the fauna of the western VFZ and that of areas further in the southwest of the Atlantic or even the Southern Ocean Weddell Sea.

4.2. Faunistic composition

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

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

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

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

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

Further north, in the South Polar Front (SPF) abundance data of macrofaunal benthic taxa sampled with an epibenthic sledge were magnitudes lower than in the Southern Ocean Weddell Sea (Brandt et al., 2007, 2012, 2014) and also in the VFZ. In the SPF, also Crustaceans dominated the macrofaunal assemblages at the stations followed by Annelida (Polychaeta) and Mollusca (Brandt et al., 2014). In this area isopod crustaceans were the dominant peracarid taxon (Meyer-Löbbecke et al., 2014). This and other peracarid taxa yielded much higher numbers of individuals in the Beagle Channel, however, from much shallower stations from the shelf (25 m) to the deep sea (663 m) with 104,618 peracarids (55,633 ind./1000 m^2), 15,025 amphipods, and 2454 tanaids (Brandt et al., 1997; 1998).

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

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

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

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2017.07.014.

References

Bober, S., et al. In this issue. Does the Mid Atlantic Ridge affect the distribution of benthic crustaceans across the Atlantic Ocean? A genetic approach on Macrostylidae and Desmosomatidae (Crustacea, Isopoda). Deep-Sea Research Part II: Topical Studies in Oceanography.

Brandt, A., 1993. Composition, abundance and diversity of peracarid crustaceans on a transect of the Kolbeinsey-Ridge, north of Iceland. Polar Biol. 13, 565–576.

Brandt, A., 1995. The Peracarida (Crustacea, Malacostraca) of the Northeast water Polynya off Greenland, documenting close pelagic-benthic coupling. Mar. Ecol. Progress. Ser. 121, 39–51.

Brandt, A., 1997. Abundance, diversity, and community patterns of epi- and benthic-boundary layer Crustacea Peracarida at 75°N of East Greenland. Polar Biol. 17, 159–174.

Brandt, A., Barthel, D., 1995. An improved supra- and epibenthic sledge for catching Peracarida (Crustacea, Malacostraca). Ophelia 43 (1), 15–23.

Brandt, A., Brenke, N., Andres, H.-G., Brix, S., Guerrero-Kommritz, J., Mühlenhardt-Siegel, U., Wägele, J.-W., 2005. Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. Org., Divers. Evol. 5, 105–112.

Brandt, A., Gooday, A.J., Brix, S.B., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Mesel, I., Diaz, R.J., Gillan, D.C., Ebbe, B., Howe, J., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Brandao, S., Pawlowski, J., Raupach, M., 2007. The Southern Ocean deep sea: first insights into biodiversity and biogeography. Nature 447, 307–311.

Brandt, A., De Broyer, C., Ebbe, B., Ellingsen, K.E., Gooday, A.J., Janussen, D., Kaiser, S., Linse, K., Schueller, M., Thomson, M.R.A., Tyler, P.A., Vanreusel, A., 2012. Southern Ocean deep benthic biodiversity. In: Rogers, Alex D., Johnston, Nadine M., Murphy, Eugene J., Andrew, Clarke (Eds.), Antarctic Ecosystems: An Extreme Environment in a Changing World, First ed. Blackwell Publishing Ltd, Oxford, pp. 291–334.

Brandt, A., Elsner, N., Golovan, O., Malyutina, M.V., Riehl, T., Schwabe, E., Würzberg, L., Brenke, N., 2013. Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems. Deep-Sea Res. II 86–87, 43–55.

Brandt, A., Elsner, N., Brenke, N., Golovan, O.A., Lavrenteva, A.V., Malyutina, M.V., Riehl, T., 2015. Abyssal macrofauna of the Kuril-Kamchatka Trench area collected by means of a camera-epibenthic sledge (Northwest Pacific). Deep-Sea Res. II 111, 175–188. http://dx.doi.org/10.1016/j.dsr2.2014.11.002.

Brandt, A., Havermans, C., Janussen, D., Jörger, K.M., Meyer-Löbbecke, A., Schnurr, S., Schüller, M., Schwabe, E., Würzberg, L., Zinkann, A.-C., 2014. Composition of epibenthic sledge catches in the South polar front of the Atlantic. Deep-Sea Res. II 108, 69–75.

Brandt, A., Mühlenhardt-Siegel, U., Siegel, V., 1998. An account of the Mysidacea (Crustacea, Malacostraca) of the Southern Ocean. Antarct. Sci. 10, 3–11.

Brandt, A., Schnack, K., 1999. Macrofaunal abundance at 79°N off East Greenland: opposing data from epibenthic-sledge and box-corer samples. Polar Biol. 22, 75–81.

Brenke, N., 2005. An epibenthic sledge for operations on marine soft bottom and bedrock. Mar. Technol. Soc. 39 (2), 13–24.

Brökeland, W., Choudhury, M., Brandt, A., 2007. Composition, abundance and distribution of Peracarida from the Southern Ocean deep sea. Deep-Sea Res. II 54, 1752–1759.

Cannat, M., 1991. A geological cross-section of the Vema fracture zone transverse ridge, Atlantic ocean. J. Geodyn. 13, 97–117.

Clarke, K.R., Gorley R.N., 2006. PRIMER v5 (& v6): User manual/tutorial, PRIMER-E, Plymouth UK, 192pp.

Dahl, E., 1954. The distribution of deep-sea Crustacea. Int. Union Biol. Sci. B 16, 43–46.

De Broyer, C., Jazdzewski, K., 1996. Biodiversity of the Southern Ocean: towards a new synthesis for the Amhipoda (Crustacea). Boll. Mus. Civico St. Nat. Verona 20, 547–568.

Devey, C. W., ed and Shipboard scientific party, 2015. RV SONNE Fahrtbericht / Cruise Report SO237 Vema-TRANSIT : bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study, Las Palmas (Spain) - Santo Domingo (Dom. Rep.) 14.12.14 - 26.01.15 GEOMAR Report, N.Ser. 023. GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, 130 pp. doi:http://dx.doi.org/10.3289/GEOMAR_REP_NS_23_2015.

Devey, C.W., Augustin, N., Brandt, A., Brenke, N., Köhler, J., Lins, L., Schmidt, C., Yeo, I. A., In this issue. Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench. Deep-Sea Research II.

Frutos I., Brandt, A., Sorbe, J.C., In press. Deep-sea suprabenthic communities: the forgotten biodiversity. In: Marine Animal Forests. The ecology of benthos biodiversity hotspots. Eds.: Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C., Springer.

Gage, J.D., Tyler, P.A., 1991. Deep-sea Biology: a Natural History of Organisms at the Deep-sea Floor. Cambridge University Press.

Guggolz, T., Lins, L., Meißner, K., Brandt, A., In this issue. Biodiversity and distribution of polychaetes (Annelida) in the Vema Fracture Zone. Deep Sea Research Part II: Topical Studies in Oceanography.

Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep sea. Deep-Sea Res. 14, 65–78.

Jamieson, A., 2015. The Hadal Zone: life in the Deepest Oceans. Cambridge University Presspp. 382.

Janussen, D., Tendal, O.S., 2007. Diversity and distribution of Porifera in the bathyal and abyssal Weddell Sea and adjacent areas. Deep-Sea Res. II 54, 1864–1875.
Kniesz, K., et al. In this issue. Peritrich ciliate epibionts on the new hadal isopod species *Macrostylis marionae* from the Puerto Rico Trench as an indicator for sex-specific behaviour. Deep-Sea Research Part II: Topical Studies in Oceanography.
Linse, K., 2006. Cruise report: JR144, 145, 146, 147 and 149. ⟨www.bodc.ac.uk⟩.
Louden, K.E., White, R.S., Potts, C.G., Forsyth, D.W., 1986. Structure and Seismotectonics of the Vema fracture-zone, Atlantic-Ocean. J. Geol. Soc. Lond. 143, 795–805 (McClain & Schlachter 2015).
McClain, C.R., Schlacher, T.A., 2015. On some hypotheses of diversity of animal life at great depths on the sea floor. Mar. Ecol. 1–24. http://dx.doi.org/10.1111/maec.12288.
Meyer-Löbbecke, A., Brandt, A., Brix, S., 2014. Diversity and abundance of deep-sea Isopoda along the Southern Polar Front: Results from the SYSTCO I and II expeditions. Deep-Sea Res. II 108, 76–84.
Morozov, E.G., Demidov, A.N., Tarakanov, R.Y., Zenk, W., 2010. Abyssal channels in the Atlantic Ocean: water structure and flows. Statew. Agric. Land Use Baseline 2015. http://dx.doi.org/10.1017/CBO9781107415324.004.
Morozov, E.G., Tarakanov, R.Y., Makarenko, N.I., 2015. Flows of Antarctic bottom water through fractures in the southern part of the North Mid-Atlantic Ridge. Oceanology 55, 796–800. http://dx.doi.org/10.1134/S0001437015060120.
Ramirez-Llodra, E., Brandt, A., Danovaro, R., Escobar, E., German, C.R., Levin, L.A., Martínez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences Discuss. 7, 2361–2485.
Riehl, T., Brenke, N., Brix, S.B., Driskell, A., Kaiser, S., Brandt, A., 2014. Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. Pol. Polar Res. 35 (2), 203–224.
Riehl, T. et al. in this issue. The effects of depth, distance, and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostylidae). Deep Sea Research Part II: Topical Studies in Oceanography.
Rintoul, S.R., Hughes, C., Olbers, D., 2001. The Antarctic circumpolar system. In: Sielder, G., Church, J., Gould, J. (Eds.), Ocean Circulation and Climate. Academic Press, Royal Society, London, pp. 271–302.
Rintoul, S.R., Meredith, M., Schofield, O., Newman, L., 2012. South. Ocean Obs. Syst. Oceanogr. 25 (3), 68–69.
Reid, J.R., 1996. On the circulation of the South Atlantic Ocean. In: Wefer, G., Berger, W.H., Siedler, G., Webb, D.J. (Eds.), The South Atlantic. Springer, Heidelberg, pp. 1–644.
Robertson, L., 2013. RRS James Cook Cruise JC094, October 13 – November 30, 2013; Tenerife – Trinidad; TROPICS - Tracing Oceanic Processes using Corals and Sediments: Reconstructing abrupt Changes in Chemistry and Circulation of the Equatorial Atlantic Ocean: Implications for global Climate and deep-water Habitats: Expedition report, 282 pp.
Schäfer, P., Ritzrau, W., Schlüter, M., Thiede, J., 2001. The Northern North Atlantic. A changing environment. Springer, Heidelberg, pp. 1–500.
Wefer, G., Berger, W.H., Siedler, G., Webb, D.J., 1996. The South Atlantic. Springer, Heidelberg, pp. 1–644.
Wilson, G.D.F., 2017. Macrofauna abundance, species diversity and turnover at three sites in the Clipperton-Clarion Fracture Zone. Mar. Biodivers. http://dx.doi.org/10.1007/s12526-016-0609-8.

Author contributions

The study was designed and conducted by Angelika Brandt.
The figures and tables were also made by Angelika Brandt. All data about polychaetes were provided by Theresa Guggolz. The manuscript was written by Angelika Brandt with subsequent contributions of Theresa Guggolz. Angelika Brandt had the idea for the project (Vema-TRANSIT) and wrote the proposals, she was the leader of the expedition.

CHAPTER 3

Biodiversity and distribution of polynoid and spionid polychaetes (Annelida) in the Vema Fracture Zone, tropical North Atlantic

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Biodiversity and distribution of polynoid and spionid polychaetes (Annelida) in the Vema Fracture Zone, tropical North Atlantic

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ABSTRACT

During the Vema-TRANSIT (Bathymetry of the Vema-Fracture Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study) expedition from December, 2014 to January, 2015, a transect along the Vema Fracture Zone in the equatorial Atlantic was surveyed and sampled at about 10°N. The Vema Fracture Zone is one of the largest fracture zones of the Mid-Atlantic Ridge and it is characterized by a large left-lateral offset. Benthic communities of the transect and the abyssal basins on both sides were investigated to examine whether the Mid-Atlantic Ridge serves as a physical barrier for these organisms, or if there is a potential connection from east to west via the Vema Fracture Zone. Samples comprised 4149 polychaetes, belonging to 42 families. Exemplary, Polynoidae and Spionidae, both typical deep-sea families with high abundances in all investigated regions, were identified up to species level. The present results show significant differences in polychaete faunistic composition between both sides of the Mid-Atlantic Ridge. Moreover, the eastern and western Vema Fracture Zone characterizes divergent habitats, since the two basins differ in sedimentology and environmental variables (e.g. temperature, salinity), hence characterizing divergent habitats. Most species found were restricted to either eastern or western VFZ, but there was a trans-Mid-Atlantic Ridge distribution of certain abundant species observed, indicating that the Mid-Atlantic Ridge might rather act limiting to dispersal between ocean basins than as an absolute barrier. Given the abyssal valley formed by the Vema Fracture Zone and its role in oceanic currents, this seafloor feature may well represent exchange routes between eastern and western faunas.

1. Introduction

The Mid-Atlantic Ridge (MAR) is an underwater mountain range dividing the Atlantic longitudinally into eastern and western basins (Murray and Hjort, 1912). With heights up to 3000 m above the seafloor, the MAR has a strong influence on the circulation of near-bottom water and therefore it is supposed to be a potential topographic barrier for the dispersal of abyssal benthic fauna (Gebruk et al., 2010; Mironov, 2006; Priede et al., 2013; McClain et al., 2009; Levin and Gooday, 2003). Recent studies investigating this barrier effect on different sides or flanks of the MAR in the North Atlantic in relation to the distribution of bathyal fauna could not find significant differences in the composition of benthic assemblages (e.g. Shields and Blanco-Perez, 2013; Bergstad et al., 2008; White et al., 2010; van der Heijden et al., 2012, Pierrot-Bults, 2008). However, these studies were focused on bathyal fauna with maximum depths around 4000 m. Thus, for the distribution of abyssal fauna, the MAR may act as a physical barrier, as vertical migration over the ridge could mean exceeding their physiological tolerance limit, such as changes in temperature and pressure (Shields and Blanco-Perez, 2013; Rex and Etter, 2010).

However, the MAR is not a continuous mountain ridge, but interrupted by several fracture zones, which result in the formation of transform faults (Ball and Harrison, 1970). Transform faults arise from two tectonic plates passing one another parallel to the plate motions. Over time, the movement causes offsets, the so-called fracture zones (van Andel et al., 1971). During the Vema-TRANSIT Expedition (Bathymetry of the Vema Fracture Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study), one of these major fracture zones of the MAR was investigated. One of the main aims of the Vema-TRANSIT Expedition was to clarify whether the MAR poses a barrier for the dispersal of abyssal fauna from eastern and western abyssal basins, and whether the Vema Fracture Zone (VFZ) can serve as a passage through the MAR for these organisms (Devey and Shipboard Scientific Party, 2015).

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Polychaetes (Annelida) are known to be one of the most abundant and diverse taxonomic groups in deep-sea samples (Fauchald and Jumars, 1979; Grassle and Maciolek, 1992). In the Vema-TRANSIT samples, polychaetes were also among the dominant taxa (Brandt et al., 2017). Furthermore, polychaetes are an interesting taxon for studies on biogeography, as they are known to possess different developmental modes with different dispersal potential (Young, 2003; Glasby et al., 2000).

In the present study, abyssal benthic polychaetes were collected along a trans-Atlantic transect at 5000 – 6000 m water depth. The aim of this study was to investigate the polychaete community structure at family and at species level for the families Spionidae and Polynoidae in the VFZ and the Vema Transform Fault (VTF) and investigate the potential barrier effect of the MAR on abyssal polychaetes belonging to the eastern and western basins.

2. Material and methods

The Vema-Transit Expedition took place from 14-12-2014 until 26-01-2015 on board of the German RV Sonne (So 237) (Devey and Shipboard Scientific Party, 2015). Samples were collected along the VFZ (Vema Fracture Zone) and VTF (Vema Transform Fault). During the cruise, the VFZ and the VTF were mapped and sampled (Fig. 1).

2.1. Study area

The VFZ is located in the tropical Atlantic (around 10°N) and originates in the VTF, which offsets the MAR by 320 km (Cannat et al., 1991; van Andel et al., 1971). The VTF has a flat floor with depths over 5000 m, covered with a thick layer of sediment (Heezen et al., 1964; Vangriesheim, 1980; Eittreim and Ewing, 1975) and bordered by steep walls with heights up to 2000 m above the valley floor (van Andel et al., 1971). The VFZ and VTF are considered to be a channel for almost the entire Antarctic Bottom Water (AABW), which is transported to the eastern Atlantic basins (Morozov et al., 2010). On the eastern side of the MAR, the southwards flowing North Atlantic Deep Water (NADW) enters the VTF, mixing with the AABW (Rhein et al., 1998).

The sediment of the eastern VFZ (eVFZ) was found to be fine and silty (Lins et al., 2016), while the western VFZ (wVFZ) was also silty, but characterized either by the presence of large manganese nodules (only station 9-2) or by manganese crusts covered with a thin sediment layer. Detailed habitat description and bathymetry of the VFZ and VTF can be found in Devey et al. (2017).

2.2. Sampling and sample treatment

Samples were collected with a camera-epibenthic sledge (C-EBS), a gear for sampling small-sized epi- and suprafauna (Brandt et al., 2013). Altogether, eleven hauls were sampled at six sites. Every haul represents a separate station, with station names combining site and haul name (e.g., station 2–6 = site 2, haul 6). As the haul length of the C-EBS varied approximately between 786 m and 2020 m, specimen counts were standardised to individual numbers per 1000 m^2 according to Devey and Shipboard Scientific Party (2015). At one station in the wVFZ (station 9-2), the EBS got stuck and the trawling distance could not be calculated as for the other stations. The flow meter data to calculate trawling distance was used instead (Brandt et al., 2017). Supra- and epinet samples per station were pooled. Based on the geographical location, all eleven stations were assigned to three different regions ("eVFZ": 2–6, 2–7, 4–8, 4–9, 6–7, 6–8; "wVFZ": 9-2, 9-8, 11-1, 11-4; "VTF": 8-4).

The content of the C-EBS was washed immediately through 300 µm sieves, stored in pre-cooled 96% ethanol, and kept for at least 48 h at −20 °C (after Riehl et al., 2014). The samples from the second station of the first site (station 2–7) and only some random subsamples (station 4–9, 6–7, 11-4) were stored in 4% formaldehyde. Specimens fixed in 96% ethanol were in appropriate condition for morphological investigations. On board, the 96% ethanol samples were sorted on ice to higher taxa level. A second sorting was performed in the home labs to retrieve specimens missed during sorting on board. Specimens were sorted and identified using compound and stereomicroscopes (100-fold magnification). Highly damaged and not identifiable specimens were labelled with the term "indet". Only anterior parts with a prostomium were counted. All polychaetes were identified at least to family level. Polynoidae and Spionidae were identified to species level (e.g. Pettibone, 1976; Sikorski and Pavlova, 2016; Maciolek, 1985). These

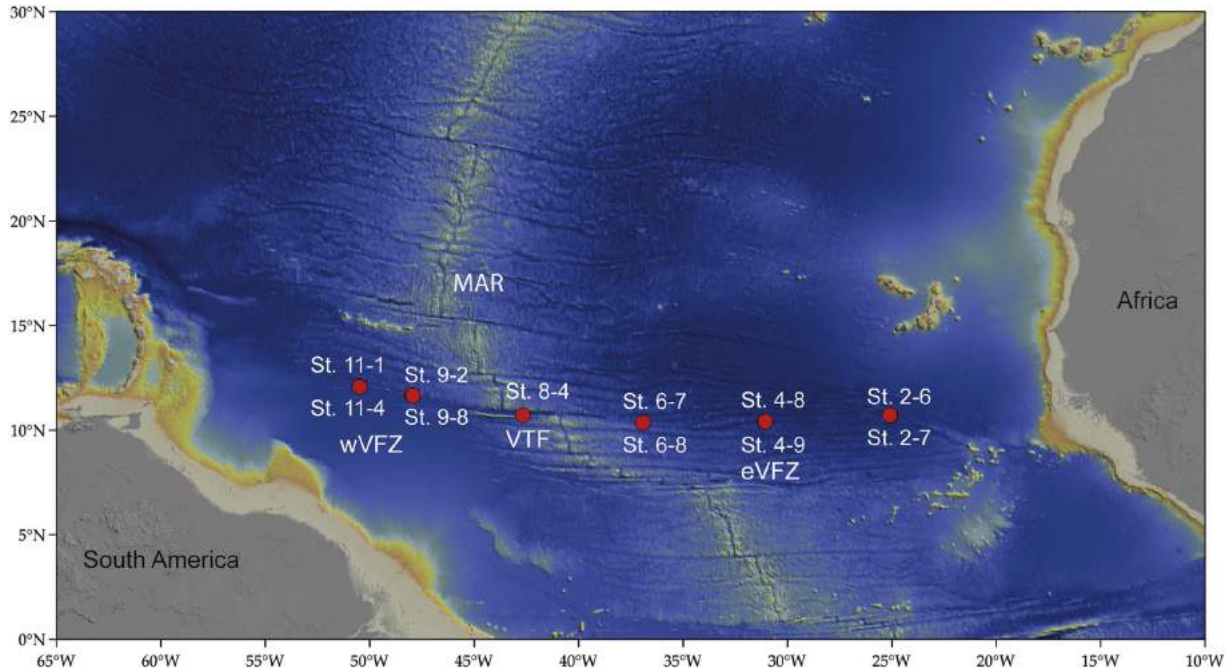

Fig. 1. Location of the stations of the Vema-Transit Expedition. wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

two families were found in high abundances in all three regions, allowing comparison between eastern and western basins and with the VTF sites. The specimens sorted to species level were given either Linnean names or preliminary names consisting of genera name plus subsequent numeration (e.g., *Laonice* sp. 1, *Laonice* sp. 2, etc.). Polynoidae and Spionidae of the Vema-Transit Expedition are deposited in the Zoological Museum of Hamburg (ZMHP). See Appendix A for a detailed species list with collection numbers.

A classification of functional groups according to feeding modes and motility defined by Jumars et al. (2015) was applied (feeding modes: surface and subsurface deposit feeders (include herbivore), carnivorous/scavengers, suspension feeder, omnivorous; motility: motile, discretely motile, sessile).

2.3. Data analysis

Statistical analyses were performed using Primer 6 (6.1.18) with the PERMANOVA + add-on (Clarke and Gorley, 2006). The polychaete multivariate matrix (standardised and log-transformed) based on densities (1000 m^2) for all higher taxa (Polynoidae and Spionidae were also analysed separately) was used in the data analyses. The VTF station (station 8-4) was excluded from the statistical analyses, as it comprised only one single station without replicates. Matrices based on Bray-Curtis similarities were used to investigate differences between different regions (eVFZ and wVFZ). Non-parametric multivariate ANOVA (PERMANOVA) was performed using a 2-factor nested design: it included 'Region' (eVFZ and wVFZ) as a fixed factor and 'station' as a random factor nested in 'Region' (Anderson and Gorley, 2007). PERMANOVA analyses on the feeding mode and motility were conducted using the same design as described above for the multivariate community analyses. Significant results were considered when $p < 0.05$. Furthermore, PERMDISP routines were performed to test the homogeneity of multivariate dispersions between stations. The results obtained by the PERMANOVA were visualised using CAP (canonical analysis of principal coordinates) plots, which discriminates *a priori* groups. SIMPER (similarity percentages) routines were performed with a 90% cut-off for low contributions in order to distinguish which groups were responsible for dissimilarities between regions. Rarefaction curves were built based on relative abundances using the Chao1 estimator, which takes in account the number of rare species. Shannon-Wiener diversity (H') was compared between regions with Kruskal-Wallis tests.

2.4. Abbreviations and terminology

C-EBS – Camera-epibenthic sledge
MAR – Mid-Atlantic Ridge
eVFZ – Eastern Vema Fracture Zone
wVFZ – Western Vema Fracture Zone
VTF – Vema Transform Fault
AABW – Antarctic Bottom Water
NADW – North Atlantic Deep Water

We are aware that the term 'family' from the Linnean Classification System is not in accordance with modern phylogeny and systematics. Nevertheless, it is still widely used in faunistic studies and in this context also used in the present study (Table 1).

3. Results

3.1. Faunistic composition

A total of 4024 polychaetes have been collected at the eleven stations of the VFZ and the VTF. Of these 4024 polychaetes, 205 specimens were non-determinable and labelled with "indet". 3819 specimens were determinable, belonging to 41 families (Table 2). The majority of the polychaetes was found in the eVFZ (3347 specimens), followed by the VTF (340 specimens), and the wVFZ (337 specimens).

Table 1
Station data of camera-epibenthic sledge from the Vema-Transit Expedition, polychaete abundance and Shannon-Wiener diversity index H'(loge) for species. eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

Station	Start Ship Position Lon [°W]	Start Ship Position Lat [°N]	End Ship Position Lon [°W]	End Ship Position Lat [°N]	depth max [m]	Towing distance DistanceTRW-W; F = Flow meter	N polychaetes Absolute numbers of individuals	N polychaetes/1000 m^2 [individuals/1000 m^2]	Shannon Diversity (species H' (loge)	Region
2–6	10° 43,17′ N	25° 4,49′ W	10° 43,80′ N	25° 3,73′ W	5520	1846	260	147	2.26	eVFZ
2–7	10° 42,06′ N	25° 4,26′ W	10° 42,94′ N	25° 3,16′ W	5507	2020	639	332	2.68	eVFZ
4–8	10° 24,96′ N	31° 5,19′ W	10° 25,63′N	31° 4,38′ W	5725	1750	666	397	2.10	eVFZ
4–9	10° 24,94′ N	31° 3,83′ W	10° 25,67′ N	31° 2,98′ W	5733	1900	870	466	2.01	eVFZ
6–7	10° 21,33′ N	36° 55,93′ W	10° 21,84′ N	36° 55,06′ W	5079	1980	383	200	2.27	eVFZ
6–8	10° 22,25′ N	36° 56,05′ W	10° 22,66′ N	36° 55,35′ W	5127	1400	586	429	1.96	eVFZ
8-4	10° 43,00′ N	42° 40,67′ W	10° 43,01′ N	42° 39,73′ W	5178	1750	343	198	2.27	VTF
9-2	11° 40,58′ N	47° 58,93′ W	11° 40,45′ N	47° 59,00′ W	4986	786_F	20	28	1.61	wVFZ
9-8	11° 39,21′ N	47° 54,96′ W	11° 39,37′ N	47° 53,98′ W	5001	1613	164	105	2.03	wVFZ
11-1	12° 5,76′ N	50° 28,85′ W	12° 5,81′ N	50° 27,96′ W	5088	1320	43	33	1.56	wVFZ
11-4	12° 4,76′ N	50° 28,94′ W	12° 4,83′ N	50° 28,14′ W	5108	1416	50	35	1.39	wVFZ

Table 2
Family composition, feeding mode and motility of the polychaetes of the Vema-Transit Expedition. Most abundant families (percent total abundance ≥5%) are highlighted in bold. Abs.no.ind. = raw individual numbers; std.no.ind. = number of individuals/1000 m^2; eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault. Feeding mode: S - surface and subsurface deposit feeders (include herbivore), C - carnivorous/scavengers, F - suspension feeder, O - omnivorous; motility: m - motile, d - discretely motile, s – sessile.

Family	N in all samples (abs.no.ind.)	N in all samples (std.no.ind.)	at n stations	% of n polychaetes in eVFZ (abs.no.ind.)	% of n polychaetes in wVFZ (abs.no.ind.)	% of n polychaetes in VTF (abs.no.ind.)	Feeding mode	motility	% of n polychaetes (abs.no.ind.)
Acrocirridae	147	92	11	3.7	3.9	3.2	S	D	3.7
Ampharetidae	118	72	11	2.5	5.0	5.0	C	D	2.9
Amphinomidae	70	37	6	2.1	0.0	0.0	S	M	1.7
Aphroditoidae	5	3	3	0.1	0.3	0.0	C	M	0.1
Arenicolidae	12	7	6	0.3	0.0	0.3	S	D	0.3
Capitellidae	98	57	10	2.5	1.8	2.4	S	M	2.4
Chrysopetalidae	28	15	7	0.8	0.3	0.0	C	M	0.7
Cirratulidae	**265**	**158**	**10**	**7.0**	**4.7**	**4.1**	**S**	**S**	**6.6**
Cossuridae	3	2	3	0.1	0.0	0.0	S	M	0.1
Dorveillidae	30	17	4	0.1	0.6	7.6	C	M,D	0.7
Eunicidae	4	2	3	0.1	0.0	0.0	S,C	M,D	0.1
fam. indet	205	71	9	3.7	21.1	2.6			5.1
Fauveliopsidae	**285**	**159**	**10**	**7.0**	**6.8**	**7.9**	**S**	**M**	**7.1**
Flabelligeridae	231	**132**	**11**	5.8	4.2	7.1	**S**	**D**	5.7
Glyceridae	104	59	7	3.0	0.3	0.3	C	M,D	2.6
Goniadidae	30	18	7	0.6	1.2	1.8	C	M,D	0.7
Hesionidae	**238**	**132**	**9**	**6.7**	**2.4**	**2.1**	**S,C**	**M,D**	**5.9**
Lacydoniidae	4	2	2	0.1	0.0	0.0	C	M	0.1
Lopadorhynchidae	20	11	5	0.6	0.0	0.0	S	M	0.5
Lumbrineridae	20	12	7	0.4	0.9	1.2	S,C	M,D	0.5
Maldanidae	16	10	8	0.3	2.1	0.0	S	D	0.4
Nephthyidae	69	38	5	2.1	0.0	0.0	C	M,D	1.7
Nereididae	17	10	6	0.4	0.3	0.3	O	M,D	0.4
Oenonidae	24	14	7	0.5	1.8	0.0	C	M,D	0.6
Onuphidae	25	13	3	0.7	0.0	0.9	S	M,D	0.6
Opheliidae	**314**	**174**	**9**	**8.1**	**2.4**	**10.0**	**S**	**M**	**7.8**
Oweniidae	11	7	6	0.2	1.2	0.0	S	D	0.3
Paraonidae	138	82	11	3.1	5.9	4.1	S	M	3.4
Pectinariidae	23	18	4	0.0	6.8	0.0	S	D	0.6
Pholoidae	12	7	6	0.3	0.3	0.0	C	M	0.3
Phyllodocidae	30	17	8	0.8	0.9	0.0	C	M	0.7
Pilargidae	18	11	6	0.3	0.6	1.8	C	M	0.4
Poecilochaetidae	16	9	8	0.3	0.6	0.9	S	D	0.4
Polynoidae	160	90	11	3.8	3.3	6.8	S,C	M,D	4.0
Sabellidae	181	105	9	4.6	3.0	5.0	F	S	4.5
Scalibregmatidae	70	38	9	1.8	1.5	1.2	S	M	1.7
Serpulidae	1	1	1	0.0	0.3	0.0	F	S	0.0
Sigalionidae	**406**	**224**	**7**	**12.0**	**0.0**	**0.9**	**C**	**M**	**10.1**
Sphaerodoridae	6	4	4	0.2	0.0	0.0	C	M,D	0.1
Spionidae	**467**	**267**	**11**	**10.8**	**12.8**	**18.5**	**S**	**M,D**	**11.6**
Syllidae	33	20	8	0.8	0.3	1.5	O	M,D	0.8
Terebellidae	70	40	9	1.6	2.7	2.6	S	M,D,S	1.7
Total	4024	2257	42						

Dominant taxa (total abundance ≥ 5%) were represented by Spionidae (11.6%), Sigalionidae (10.1%), Opheliidae (7.8%), Fauveliopsidae (7.1%), Cirratulidae (6.6%), Hesionidae (5.9%), and Flabelligeridae (5.7%) (Table 2). Spionidae was the most abundant family in all three regions. Sigalionidae was present in the eVFZ and in the VTF. Opheliidae was more abundant in the eVFZ and the VTF, but less abundant in the wVFZ. Fauveliopsidae, Cirratulidae, Hesionidae and Flabelligeridae were collected from all three regions, with slight differences in abundance between regions (Table 2).

All regions exhibited similar polychaete feeding types and motility composition between regions (Fig. 2A, B). Between 33% and 40% of the polychaete community was characterized by subsurface and surface deposit feeders in all three regions. In addition, carnivore and/ or scavengers accounted for 33–37% of relative abundances in all three regions (Fig. 2A). The average majority of the polychaete community in all three regions was motile (33–47%), with the highest contribution of this group in the VTF. Around 30% were a mix between discretely motile and motile. Discretely motile polychaetes accounted for 18–26% of the polychaetes, with highest numbers observed in the wVFZ (Fig. 2B).

Considering samples identified up to species level, a total of 584 spionids were found for all sites, belonging to 5 different genera and 18 different species. 117 specimens were non-determinable and labelled with “indet”. The most abundant species (total abundance of spionids ≥ 5%) were *Aurospio* aff. *dibranchiata* Maciolek, 1981 (189 specimens, 40.5%), *Prionospio* sp. 8 (70 specimens, 15%), *Laonice* aff. *blakei* Sikorski and Jirkov in Sikorski et al., 1988 (64 specimens, 13.7%), *Spiophanes longisetus* Meißner, 2005 (35 specimens, 7.5%), and *Prionospio* sp.1 (27 specimens, 5.8%) (Table 3).

Regarding the three regions, only 2.8% of the spionid specimens were unique for one of the sites, while 80.1% of the specimens were trans-MAR (occurred in the eVFZ and the wVFZ) (Fig. 3A). 17.1% of the specimens were found to be widespread (occurred at least at two different sites in one region) (Fig. 3A). Eight spionid species were unique, four species were widespread and six species were found to be trans-MAR (Fig. 3B). Most of the unique species (five species) were found in the eVFZ, whereas only two species were restricted to the wVFZ and one species was found to be unique for the VTF.

A total of 165 polynoids were found, belonging to 32 species of seven different genera and two subfamilies. Five specimens were non-

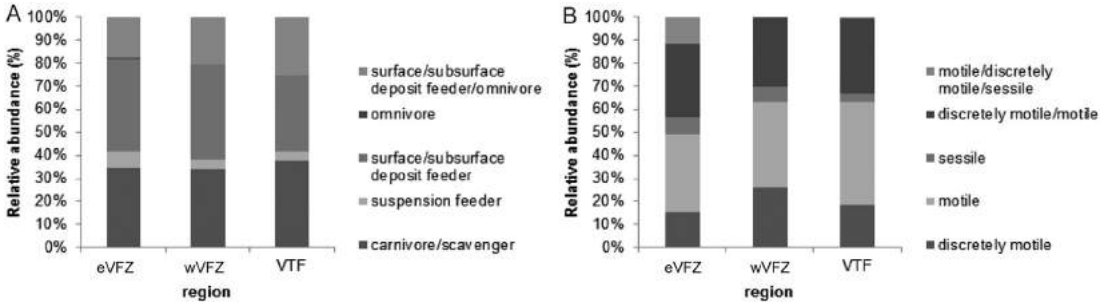

Fig. 2. A. Relative abundance of polychaete feeding types at each region. B. Relative abundance of polychaete motility at each region. eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

determinable and labelled with "indet". The most abundant species (total abundance of polynoids ≥ 5%) were aff. *Bathyedithia* sp. 1 (55 specimens, 34.4%), *Bathypolaria carinata* Levenstein, 1981 (24 specimens, 15.0%), *Bathyfauvelia* sp. 1 (13 specimens, 8.1%), and *Bathypolaria* sp. 1 (ten specimens, 6.3%) (Table 4).

Considering all polynoid specimens obtained, 19.4% were unique for one of the sites, 63.8% were trans-MAR and 16.9% of the specimens were widespread (Fig. 3A). 21 polynoid species were found to be unique, five were widespread and six species occurred as trans-MAR. Most of the unique species (13 species) were found in the eVFZ, only six species were unique for the wVFZ, and two species were found to be unique for the VTF.

3.2. Data analysis

For Polynoidae and Spionidae species, Shannon Diversity varied between 1.39 and 2.68 (Table 1) with no significant differences between the regions ($x^2(10) = 10$, $p < 0.65$).

The results for the polychaete multivariate assemblages at family level based on relative abundances significantly differed between regions ($p < 0.009$). PERMDISP results were not significant at the family level multivariate matrix. Based on the SIMPER results, main differences between eVFZ and wVFZ were derived from higher densities of Pectinariidae in the wVFZ (12.8%), which was completely absent in the eVFZ, and of Sigalionidae in the eVFZ (9%), absent in the wVFZ. These two regions exhibited an average dissimilarity of 53.9%. Rarefaction curves for eVFZ and wVFZ separately did not reach an asymptote

Table 3
Polynoidae species composition of the different regions of the Vema-Transit Expedition. Most abundant species (percent total abundance ≥5%) in all three regions are highlighted in bold. Abs.no.ind. = raw individual numbers; std.no.ind. = number of individuals/1000 m^2; eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

Taxa/regions		eVFZ		wVFZ		VTF		Total		% of n Polynoidae
	abs.no.ind.	std.no.ind.	abs.no.ind.	std.no.ind.	abs.no.ind.	std.no.ind.	abs.no.ind.	std.no.ind.	abs.no.ind.	std.no.ind.
aff. *Bathyfauvelia* sp.1	0	0	1	1	0	0	1	1	0.6	1.4
aff. *Bathyedithia* sp.1	**40**	**22**	**1**	**1**	**14**	**8**	**55**	**31**	**34.4**	**34.5**
aff. *Bathyedithia* sp.2	1	1	0	0	0	0	1	0	0.6	0.6
aff. *Macellicephala* sp.1	2	1	0	0	0	0	2	1	1.3	1.1
aff. *Macellicephala* sp.2	3	2	0	0	0	0	3	2	1.9	1.9
Bathyedithia sp.1	3	2	1	1	1	1	5	3	3.1	3.0
Bathyedithia sp.2	0	0	1	1	0	0	1	1	0.6	0.7
Bathyedithia sp.3	1	1	0	0	0	0	1	1	0.6	0.6
Bathyedithia sp.4	0	0	1	1	0	0	1	1	0.6	0.8
***Bathyfauvelia* sp.1**	**12**	**7**	**1**	**1**	**0**	**0**	**13**	**8**	**8.1**	**8.4**
Bathypolaria carinata	**10**	**5**	**0**	**0**	**0**	**0**	**10**	**5**	**6.3**	**5.8**
***Bathypolaria* sp. 1**	**21**	**12**	**1**	**1**	**2**	**1**	**24**	**14**	**15.0**	**15.3**
Bruunilla sp.1	3	1	0	0	0	0	3	1	1.9	1.7
Bruunilla sp.2	1	1	0	0	0	0	1	1	0.6	0.6
Bruunilla sp.3	2	1	0	0	0	0	2	1	1.3	1.1
Bruunilla sp.4	0	0	0	0	2	1	2	1	1.3	1.3
Bruunilla sp.5	2	1	0	0	0	0	2	1	1.3	1.1
Bruunilla sp.6	0	0	0	0	1	1	1	1	0.6	0.6
Bylgides sp.1	1	1	1	1	0	0	2	2	1.3	2.0
Macellicephalinae sp. 4	1	1	0	0	0	0	1	1	0.6	0.8
Macellicephalinae sp. 5	1	1	0	0	0	0	1	1	0.6	0.8
Macellicephalinae sp.1	0	0	1	1	1	1	2	1	1.3	1.3
Macellicephalinae sp.2	2	1	1	1	0	0	3	2	1.9	2.0
Macellicephalinae sp.3	0	0	0	0	1	1	1	1	0.6	0.6
Macellicephaloides sp. 1	3	1	0	0	0	0	3	1	1.9	1.7
Macellicephaloides sp. 2	1	1	0	0	0	0	1	1	0.6	0.6
Macellicephaloides sp. 3	1	0	0	0	0	0	1	0	0.6	0.6
Macellicephaloides sp. 5	2	1	0	0	0	0	2	1	1.3	1.2
Macellicephaloides sp. 6	7	3	0	0	1	1	8	4	5.0	4.5
Macellicephaloides sp. 7	4	2	0	0	0	0	4	2	2.5	2.2
Polaruschakovinae sp.1	0	0	1	1	0	0	1	1	0.6	0.7
Polaruschakovinae sp.2	2	1	0	0	0	0	2	1	1.3	1.2
Total	138	97	25	17	13	13	160	90		

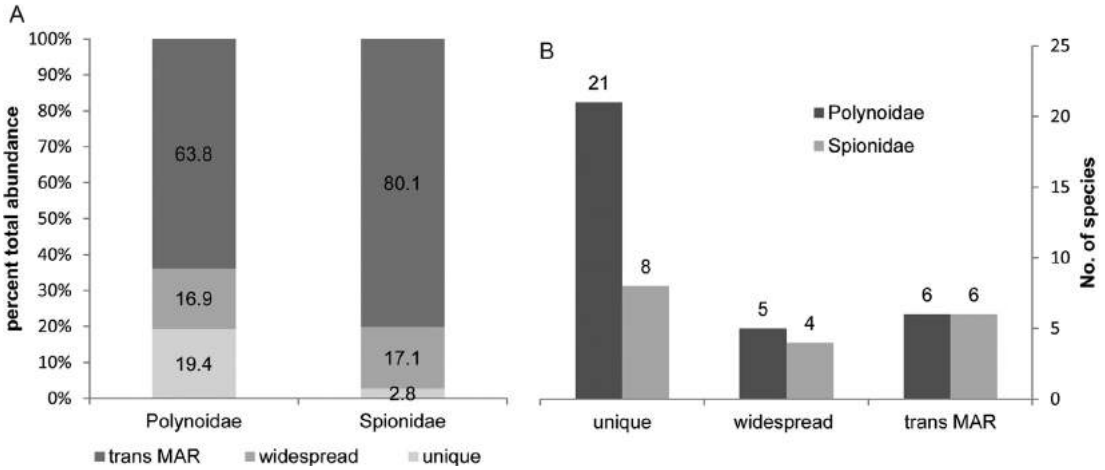

Fig. 3. Unique, widespread, and ubiquitous polynoids and spionids among the Vema Fracture Zone and Vema Transform Fault. Percent total abundance (left axis) and number of species (right axis) given for each category. Unique = species present in one site; widespread = species occurring at least in two different sites in one region; ubiquitous = species occurring in the eastern and western VFZ.

Table 4
Spionidae species composition of the different regions of the Vema-Transit Expedition. Most abundant species (percent total abundance ≥ 5%) in all three regions are highlighted in bold. Abs.no.ind. = raw individual numbers; std.no.ind. = number of individuals/1000 m^2; eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

Taxa/regions	eVFZ		wVFZ		VTF		total		% of n Spionidae	
	abs.no.ind.	st.no.ind.	abs.no.ind.	st.no.ind.	abs.no.ind.	st.no.ind.	abs.no.ind.	st.no.ind.	abs.no.ind.	st.no.ind.
aff. *Lindaspio* sp. 1	6	4	0	0	1	1	7	5	1.5	1.7
aff. *Lindaspio* sp. 2	0	0	0	0	2	1	2	1	0.4	0.4
Aurospio* aff. *dibranchiata	159	90	10	6	20	11	189	107	40.5	40.2
***Laonice* sp. 2**	1	0	0	0	0	0	1	0	0.2	0.2
Laonice sp. 1	4	2	0	0	0	0	4	2	0.9	0.8
Laonice aff. *blakei*	35	20	13	9	16	9	64	38	13.7	14.3
Laonice sp. 4	1	1	0	0	0	0	1	1	0.2	0.2
Laonice sp. 5	2	1	1	1	0	0	3	2	0.6	0.9
Laonice sp. 6	0	0	1	1	0	0	1	1	0.2	0.5
***Prionospio* sp. 1**	23	12	0	0	4	2	27	15	5.8	5.5
Prionospio sp. 2	1	1	0	0	0	0	1	1	0.2	0.2
Prionospio sp. 3	11	6	0	0	4	2	15	8	3.2	3.1
Prionospio sp. 4	0	0	2	2	0	0	2	2	0.4	0.6
Prionospio sp. 5	1	1	0	0	0	0	1	1	0.2	0.2
Prionospio sp. 7	11	6	2	1	0	0	13	7	2.8	2.7
***Prionospio* sp. 8**	53	29	7	5	10	6	70	39	15.0	14.6
Prionospio sp. 9	27	14	0	0	4	2	31	17	6.6	6.2
Spiophanes longisetus	26	15	7	4	2	1	35	21	7.5	7.8
Total	361	201	43	29	63	36	467	267		

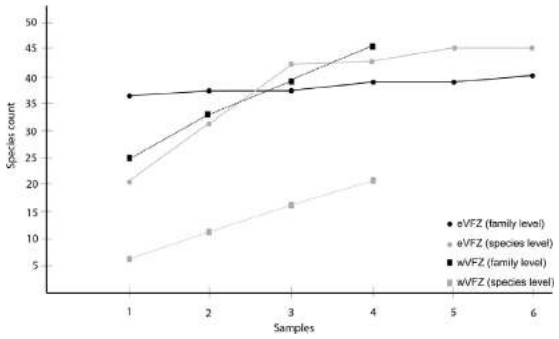

Fig. 4. Rarefaction curves for polychaetes from the Vema-TRANSIT Expedition based on relative abundances using the Chao1 estimator. eVFZ = eastern Vema Fracture Zone; wVFZ = western Vema Fracture Zone, VTF = Vema Transform Fault.

(Fig. 4). CAP results at family level can be observed in Fig. 5A. Furthermore, a higher variability between stations was observed for the wVFZ region when compared with the eVFZ.

PERMANOVA results on the feeding mode and motility at family level did not reveal significant differences between eVFZ and wVFZ ($p > 0.3164$ and $p > 0.08$, respectively).

PERMANOVA results for species of Spionidae and Polynoidae revealed significant differences between regions for both families together ($p < 0.0042$). PERMDISP results were significant at species level ($p < 0.0051$), indicating that differences observed might be due to the dispersion of the data. SIMPER revealed higher contributions from the species *Aurospio* aff. *dibranchiata* and aff. *Bathyedithia* sp. 1 in the eVFZ (together they accounted for 22.7% of the total dissimilarity), and from *Laonice* aff. *blakei*, *Prionospio* sp. 8, and *Spiophanes longisetus* in the wVFZ (responsible for 24.1% of the total dissimilarity). Communities differed 75.2% between eVFZ and wVFZ according to the SIMPER results. Rarefaction curves at species level reached an asymptote for the eVFZ stations, but not for the wVFZ stations (Fig. 4). CAP results for the level of species can be found in Fig. 5B.

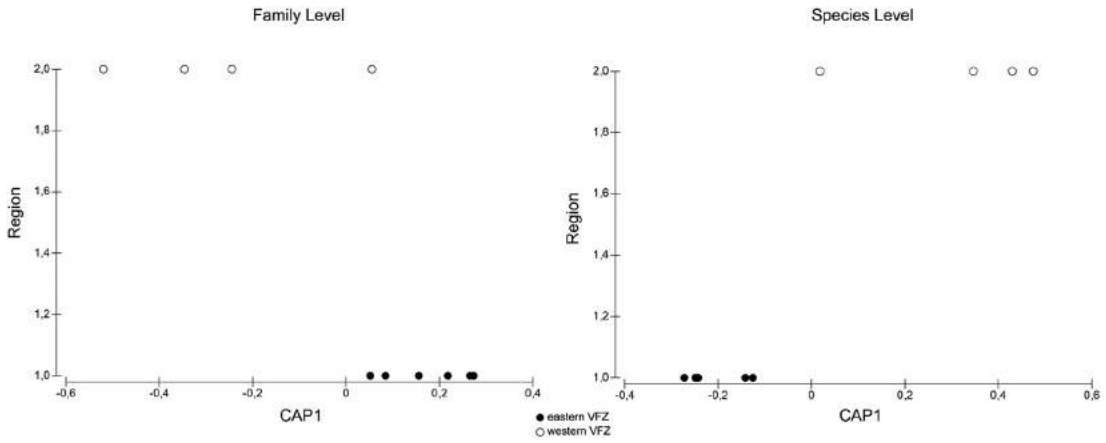

Fig. 5. Canonical analysis of principal coordinates (CAP) based on standardized Bray-Curtis similarities (A) from polychaete families and from (B) polynoid and spionid species of the Vema-TRANSIT Expedition. VFZ = Vema Fracture Zone.

Similarly to the results obtained at family level, higher variability between stations was observed for the wVFZ when compared with the eVFZ.

4. Discussion

4.1. Faunistic composition

In this study, major differences in the abundance of polychaetes between the eVFZ, wVFZ and VTF were observed. In total, the wVFZ contributed only with 8.4% of the total numbers of polychaetes found in the samples of the Vema-TRANSIT. This is a major difference compared to the 83.2% of specimens coming from the eVFZ. In total, more stations were sampled in the eVFZ (six stations) than in the wVFZ (four stations), but even at the single station in the VTF the same percentage of polychaetes (8.4%) were found as in the wVFZ. These low abundances in the wVFZ were also reported for other macrofaunal taxa from the C-EBS samples (Brandt et al., 2017). Differences in abundance between areas might have been originated from differences in sediment structure between the different regions (Devey et al., 2017). While the eastern stations were mainly characterized by deep-sea soft sediments, the western stations exhibited both silty sediments and manganese nodules and crusts, which increased sediment and habitat heterogeneity. The presence of hard structures might have influenced in both the low retrieve of organisms, as well as in their lower abundances observed in the wVFZ in comparison with the eastern stations. Also, it has to be taken into account that he EBS is known to be suitable for qualitative but not for quantitive sampling (Brenke, 2005; Schüller et al., 2009), and a possible sampling bias caused by the hard substrate and the manganese nodules in the wVFZ could be another reason for the divergence observed between regions. The fact that rarefaction curve for the eVFZ reached an asymptote indicates that the sampling was sufficient to represent the species composition in this habitat, while at the wVFZ stations more sampling is needed. Nevertheless, although comparisons involving total abundances of species between regions might not be possible due to species that might have been undersampled or missed, comparisons between the faunistic compositions are still possible.

In this study, most of the polychaetes and other macrofaunal taxa sampled in the VTF and VFZ (Brandt et al., 2017) were bottom-dwelling organisms with preference for soft-bottom sediments, which was mainly observed in the eVFZ. Here, the significant differences in family composition between the eVFZ and wVFZ were mainly based on the restriction of Sigalionidae and Pectinariidae to one of the regions. Sigalionidae was only present in the eVFZ, and this pattern may be explained by their preference for soft sediments (Jumars et al., 2015), which characterized this area (Lins et al., 2016). On the contrary, Pectinariidae generally has a preference for larger grains for constructing their tubes (Jumars et al., 2015). Therefore, the coarser sediment found in the wVFZ compared to the sediment in the eVFZ (except site 2) (Lins et al., 2016) could be an explanation for the restriction of this group to the wVFZ.

The composition of the polychaete community from the VFZ was comparable to that of other deep-sea studies at family level. Spionidae is one of the most abundant families in the abyss and it was previously reported for different deep-sea areas (Glover et al., 2001; Cosson-Sarradin et al., 1998). Opheliidae, Cirratulidae, and Fauveliopsidae are also commonly abundant deep-sea taxa (Thiel et al., 2011; Fiege et al., 2010), as well as Flabelligeridae, which was reported as abundant at an oligotrophic deep-sea Atlantic site (Cosson-Sarradin et al., 1998). The results obtained for Pectinariidae, as the second most abundant family in the wVFZ (Table 1), were rather uncommon, as this family has only been reported in high abundances for shelf environments, while being scarcely represented in the deep sea (Levin et al., 2000).

Functional groups of polychaetes showed no differences across the different studied regions. No significant differences in either feeding strategy or motility of the polychaetes between regions were found. The abundance of deposit feeders, followed by carnivores in this study is not surprising, as this was observed to be common in other deep-sea areas as well (Fiege et al., 2010; Hessler and Jumars, 1974; Kröncke et al., 2003; Kröncke and Türkay, 2003).

At species level, there was a significant difference in the species composition between the eVFZ and wVFZ. Nevertheless, PERMDISP results were also significant, meaning that part of the differences found could be derived from dispersion of the data and not due to real faunistic differences between regions. At species level, the Shannon-Wiener diversity was comparable to other deep-sea studies, with values between 1.39 and 2.68 (Schüller et al., 2009; Hilbig and Blake, 2006; Cosson-Sarradin et al., 1998). Even if no significant differences of diversity were found between the regions values were slightly lower for the wVFZ. This is an interesting observation, as a high variability especially for the western stations, would be expected based on the higher habitat heterogeneity in this region due to the presence of manganese nodules and crusts. This higher habitat heterogeneity could have an influence in how polychaete communities are distributed and it might also favour niche segregation and increases in diversity. The positive influence of increasing sediment heterogeneity on abyssal macrofauna was already suggested by Etter and Grassle (1992), as they found a strong correlation between species diversity and sediment diversity. The lack of correlations between habitat heterogeneity and diversity observed may be influenced by the low polychaete abundance found in the wVFZ, which might have been due to undersampling, and

also by the low resolution in identification for most of the families. In this study, only two families were chosen as model organisms and further determined to species level.

However, even if the majority of the species found (belonging to the families Polynoidae and Spionidae) were unique to one region, both eVFZ and wVFZ regions were dominated by a small group of trans-MAR species. Most of these trans-MAR species (*Spiophanes longisetus*, *Aurospio* aff. *dibranchiata*, *Laonice* aff. *blakei,* aff. *Bathyedithia* sp.1) were morphologically very similar to species recorded for the Atlantic before, or belong to typical deep-sea genera (Maciolek, 1981; Sikorski, 2003; Meißner, 2005; Pettibone, 1976). This pattern of a small group of widespread species with high abundance and a larger group of unique, rare species was previously reported for polychaetes in the Atlantic, Southern Ocean, and Pacific (Glover et al., 2001, 2002; Fiege et al., 2010). There, the high number of rare species in the abyss was considered to be an evidence for either high species turnover or an effect of undersampling (Glover et al., 2001; Fiege et al., 2010).

4.2. Distribution patterns

The significant differences in family and species composition between the eVFZ and wVFZ might have been mainly derived from the considerable abiotic disparities observed between these habitats. The wVFZ is influenced by the AABW, resulting in lower temperatures, higher conductivity, and slightly higher concentrations of dissolved oxygen compared to the eVFZ, characterized by the warmer and more salty NADW (Devey et al., 2017). In addition, as described above, the substrate type also differed between regions, with fine and silty sediments present in the eVFZ and hard substratum and a small layer of larger grain-sized sediment in the wVFZ (Lins et al., 2016). Despite these differences, shared species occurred in high abundances in all habitats next to many unique species with low abundance. Widespread distribution is common for many other benthic deep-sea groups, such as holothurians, foraminifers and nematodes, but also for polychaetes (McClain and Hardy, 2010; Bisol et al., 1984; Mincks et al., 2009; Pawlowski et al., 2007; Vanreusel et al., 2010; Fiege et al., 2010). These widespread species are supposed to be opportunistic, as they have to be able to adapt to different habitats with changing environmental conditions (Glover et al., 2001).

It is assumed that one important advantage for species dispersal and distribution in the abyss is the ability of many deep-sea taxa to develop via planktonic larval stages (Young et al., 1997; Yearsley and Sigwart, 2011; Hilário et al., 2015), as dispersal distance can be large for relatively non-motile adult marine taxa (McClain and Hardy, 2010). Especially in cold deep-sea waters, low metabolism may be a driving factor for increasing distances of larval dispersal (Rex et al., 2005). In the present study, the Polynoidae and Spionidae analysed at species level are both known to have, next to other development strategies, planktonic larval stages, although the knowledge about developmental biology of deep-sea polychaetes is still sparse (Giangrande, 1997; Wilson, 1991; Blake and Arnofsky, 1999). Nevertheless, it is suggested that the type of development of species can be forecast based on other species of the genera (Blake, 2006).

Several studies, concerning dispersal of abyssal planktonic larvae, showed at least a certain level of migration between habitats separated by potential topographic barriers such as ridges, rises, or even fracture zones (bivalvia: Zardus et al., 2006; Etter et al., 2011; van der Heijden et al., 2012; Olu et al., 2010; polychaetes: Plouviez et al., 2010). Even brooding non-swimming isopods showed sporadic connectivity across the MAR in the eastern South Atlantic abyss, with water masses flowing through the deep Romanche Fracture Zone acting as a supposed connection bridge (Brix et al., 2015). Also isopods species from the Vema-TRANSIT Expedition occurred both in the eVFZ and in the wVFZ, although the gene flow between eVFZ and wVFZ seems to be restricted (Bober et al., 2017, Riehl et al., 2017), indicating that dispersion might be species or taxa-specific.

Actually, the distribution of many species with planktonic larvae might not be limited by restricted dispersal capabilities, but rather by extrinsic factors. Thus, even if the larvae can migrate between the eVFZ and the wVFZ, factors like sedimentology, temperature and salinity could prevent their successful settlement (e.g. Pawlik, 1992; Eckman, 1996; Tyler and Young, 1998) as well as intra- or interspecific competition (e.g. Jumars, 1976). This would explain the less abundant but diverse unique species and the small number of trans-MAR species with high abundance in the studied regions. However, this distribution pattern may have been biased by the generally low abundances of these unique species and thus the possibility that these species have been missed given the limited sampling conducted. The trans-MAR distribution of certain species, however, indicates that the MAR is not an absolute barrier for species dispersal. Given the abyssal valley formed by the VFZ and other such plate boundaries, these seafloor features may well represent exchange routes between eastern and western faunas. Taking into account that the depth of the VFZ and VTF are comparable between eastern and western abyssal plains (van Andel et al., 1971) and vertical migration of abyssal specimens over the MAR would be beyond the physiological tolerances of most abyssal taxa (Rex and Etter, 2010; Menzies et al., 1973), a likely way is their transport through the VFZ and VTF.

The potential role of the VFZ as a connection through the MAR is also supported by its important role in the circulation of near bottom water, as there is an eastward flow of the AABW (Levin and Gooday, 2003; Eittreim and Ewing, 1975; Mauritzen et al., 2002). Together with the NADW, these currents seem to support even non-swimming taxa to be passively transported through the water column between the eVFZ and wVFZ (Lins et al., 2016).

4.3. Conclusion

The results obtained from this research indicate that the MAR might not represent an absolute barrier for the dispersal of organisms, as shared species were encountered east and west of the MAR. The dispersal of organisms between eVTF and wVTF likely occurs through the VTF and their passive transport aided by the deep currents AABW and NADW. Furthermore, the results obtained for polychaete abundances and diversity for both areas might have been biased by the differences in sampling effort between areas and should be interpreted carefully. Molecular studies on the sampled polychaetes are expected in the future, and these will help to elucidate whether the same morphological species found in both sides of the MAR are actually the same species or rather cryptic species.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2017.07.013.

References

Anderson, M.J., Gorley, R.N., 2007. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.

Ball, M.M., Harrison, C.A., 1970. Crustal plates in the central Atlantic. Science 167 (3921), 1128–1129.

Bergstad, O.A., Menezes, G., Høines, A.S., 2008. Demersal fish on a mid-ocean ridge: distribution patterns and structuring factors. Deep-Sea Res. Part II 55, 185–202.

Bisol, P.M., Costa, R., Sibuet, M., 1984. Ecological and genetical survey of two deep-sea holothurians: *Benthogone rosea* and *Benthodytes typica*. Mar. Ecol. Prog. Ser. 15, 275–281.

Blake, J.A., 2006. Spionida. In: Rouse, G., Pleijel, F. (Eds.), Reproductive Biology and Phylogeny of Annelida. Science Publishers, Enfield, pp. 565–638.

Blake, J.A., Arnofsky, P.L., 1999. Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. Hydrobiologia 402, 57–106.

Bober, S., Riehl, T., Brandt, A., 2017. Does the Mid-Atlantic Ridge affect the distribution of benthic crustaceans across the Atlantic Ocean? Deep-Sea Res II (in this issue).

Brandt, A., Elsner, N., Golovan, O., Malyutina, M.V., Riehl, T., Schwabe, E., Würzberg, L., Brenke, N., 2013. Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems. Deep-Sea Res. II 86–87, 43–55.

Brandt, A., Frutos, I., Bober, S., Brix, S., Brenke, N., Guggolz, T., Heitland, N., Malyutina, M., Minzlaff, U., Riehl, T., Schwabe, E., Zinkann, A.-C., Linse, K., 2017. Composition of abyssal macrofauna along the Vema Fracture Zone and the hadal Puerto Rico Trench northern tropical Atlantic collected by means of a camera-epibenthic sledge. Deep-Sea Res II (in this issue).

Brenke, N., 2005. An epibenthic sledge for operations on marine soft bottom and bedrock. Mar. Technol. Soc. 39 (2), 13–24.

Brix, S., Leese, F., Riehl, T., Kihara, T.C., 2015. A new genus and new species of Desmosomatidae Sars, 1897 (Isopoda) from the eastern South Atlantic abyss described by means of integrative taxonomy. Mar. Biodivers. 45 (1), 7–61.

Cannat, M., Mamaloukas-Frangoulis, V., Auzende, J.M., Bideau, D., Bonatti, E., Honnorez, J., Lagabrielle, Y., Malavieille, J., Mevel, C., 1991. A geological cross-section of the Vema fracture zone transverse ridge, Atlantic ocean. J. Geodyn. 13 (2), 97–117.

Clarke, K.R., Gorley, R.N., 2006. User Manual/Tutorial. Primer-E Ltd., Plymouth, pp. 93.

Cosson-Sarradin, N., Sibuet, M., Paterson, G.L.J., Vangriesheim, A., 1998. Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. Mar. Ecol. Prog. Ser. 165, 173–185.

Devey, C.W., Augustin, N., Brandt, A., Brenke, N., Köhle, J., Lins, L., Schmidt, C., Yeo, I.A., 2017. Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench. Deep-Sea Res. II (in this issue).

Devey, C.W., ed., Shipboard Scientific Party, 2015. RV SONNE Fahrtbericht/Cruise Report SO237 Vema-TRANSIT. GEOMAR Report, N. Ser. 023. GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, pp. 130.

Eckman, J.E., 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. J. Exp. Mar. Biol. Ecol. 200 (1), 207–237.

Eittreim, S., Ewing, J., 1975. Vema fracture zone transform fault. Geology 3 (10), 555–558.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360, 576–578.

Etter, R.J., Boyle, E.E., Glazier, A., Jennings, R.M., Dutra, E., Chase, M.R., 2011. Phylogeography of a pan-Atlantic abyssal protobranch bivalve: implications for evolution in the Deep Atlantic. Mol. Ecol. 20 (4), 829–843.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 17, 193–284.

Fiege, D., Ramey, P.A., Ebbe, B., 2010. Diversity and distributional patterns of Polychaeta in the deep South Atlantic. Deep Sea Res. Part I 57 (10), 1329–1344.

Gebruk, A.V., Budaeva, N.E., King, N.J., 2010. Bathyal benthic fauna of the Mid-Atlantic Ridge between the Azores and the Reykjanes Ridge. J. Mar. Biol. Assoc. UK 90 (01), 1–14.

Giangrande, A., 1997. Polychaete reproductive patterns, life histories: an overview. Oceanography and marine Biology. Annu. Rev. 35, 323–386.

Glasby, C.J., Hutchingsen, P.A., Fauchald, K., Paxton, H., Rouse, G.W. Watson Russell, C., Wilson, R.S., 2000. Class polychaeta. In: Polychaetes & Allies: The Southern Synthesis. Fauna of Australia.CSIRO Publishing, Melbourne. pp. 1–296.

Glover, A., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Sheader, M., 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. Mar. Ecol. Prog. Ser. 240, 157–170.

Glover, A.G., Paterson, G.L.J., Bett, B.J., Gage, J.D., Sibuet, M., 2001. Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. Deep-Sea Res. I 48, 217–236.

Grassle, J.F., Maciolek, N.J., 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. Am. Nat. 313–341.

Heezen, B.C., Gerard, R.D., Tharp, M., 1964. The Vema fracture zone in the equatorial Atlantic. J. Geophys. Res. 69 (4), 733–739.

Hessler, R.R., Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central north Pacific. In: Deep Sea Research and Oceanographic Abstracts. Elsevier 21(3), pp. 185–209.

Hilário, A., Metaxas, A., Gaudron, S.M., Howell, K.L., Mercier, A., Mestre, N.C., Ross, R.E., Thurnherr, A.M., Young, C., 2015. Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Front. Mar. Sci. 2 (6).

Hilbig, B., Blake, J.A., 2006. Deep-sea polychaete communities in the northeast Pacific Ocean off the Gulf of the Farallones, California. Bull. Mar. Sci. 78 (2), 243–269.

Jumars, P.A., 1976. Deep-sea species diversity: does it have a characteristic scale. J. Mar. Res. 34 (2), 217–246.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Mar. Sci. 7.

Kröncke, I., Türkay, M., 2003. Structural and functional aspects of the benthic communities in the deep Angola Basin. Mar. Ecol. Prog. Ser. 260, 43–53.

Kröncke, I., Türkay, M., Fiege, D., 2003. Macrofauna communities in the eastern Mediterranean deep sea. Mar. Ecol. 24 (3), 193–216.

Levenstein, R.Y., 1981. Some Pecularities of the Distribution of the Family Polynoidae from the Canada Basin of the Arctic ocean. 115. Academy of Sciences of the USSR. Transactions of the P.P.Shirshov.Institute of Oceanologypp. 26–36.

Levin, L.A., Gooday, A.J., 2003. The deep atlantic ocean. In: Goodall, D.W. (Ed.), Ecosystems of the World. Elsevier Scientific, Amsterdam, pp. 111–178.

Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macrobenthic community structure within and beneath the oxygen minimum zone. NW Arab. Sea. Deep-Sea Res. Part II 47 (1), 189–226.

Lins, L., da Silva, M.C., Neres, P., Esteves, A.M., Vanreusel, A., 2016. Testing deep-sea biodiversity paradigms on abyssal nematode genera and Acantholaimus species. Deep-Sea Res. II.

Maciolek, N.J., 1981. A new genus and species of Spionidae (Annelida: Polychaeta) from the north and south Atlantic. Proc. Biol. Soc. Wash. 94, 228–239.

Maciolek, N.J., 1985. A revision of the genus *Prionospio* Malmgren, with special emphasis on species from the Atlantic Ocean, and new records of species belonging to the genera *Apoprionospio* Foster and *Paraprionospio* Caullery (Polychaeta, Annelida, Spionidae). Zool. J. Linn. Soc. 84 (4), 325–383.

Mauritzen, C., Polzin, K.L., McCartney, M.S., Millard, R.C., West-Mack, D.E., 2002. Evidence in hydrography and density fine structure for enhanced vertical mixing over the Mid-Atlantic Ridge in the western Atlantic. J. Geophys. Res. Oceans 107 (C10).

McClain, C.R., Hardy, S.M., 2010. The dynamics of biogeographic ranges in the deep sea. Proc. R. Soc. Lond. B Biol. Sci. 277 (1700), 3533–3546.

McClain, C.R., Rex, M.A., Etter, R.J., 2009. Deep-sea macroecology. In: Witman, J.D., Roy, K. (Eds.), Marine Macroecology. University of Chicago Press, Chicago, IL, pp. 65–100.

Meißner, K., 2005. Revision of the genus *Spiophanes* (Polychaeta, Spionidae); with new synonymies, new records and descriptions of new species. Mitt. Mus. Nat. Berl. Zool. Reihe 81, 3–65.

Menzies, R.H., George, R.Y., Rowe, G.T., 1973. Abyssal Environment and Ecology of the World Oceans. Wiley-Interscience, New York.

Mincks, S.L., Dyal, P.L., Paterson, G.L.J., Smith, C.R., Glover, A.G., 2009. A new species of *Aurospio* (Polychaeta, Spionidae) from the Antarctic shelf, with analysis of its ecology, reproductive biology and evolutionary history. Mar. Ecol. 30, 181–197.

Mironov, A.N., 2006. Echinoids from seamounts of the north-eastern Atlantic; onshore/offshore gradients in species distribution. In: Mironov, A.N., Gebruk, A.V., Southward, A.J. (Eds.), Biogeography of the North Atlantic seamounts. KMK Scientific Pres Ltd, pp. 96–133.

Morozov, E.G., Demidov, A.N., Tarakanov, R.Y., Zenk, W., 2010. Abyssal Channels in the Atlantic Ocean: Water Structure and Flows. Springer Science & Business Media.

Murray, J., Hjort, J., 1912. The Depths of the Ocean. McMillan, London, pp. 812.

Olu, K., Cordes, E.E., Fisher, C.R., Brooks, J.M., Sibuet, M., Desbruyères, D., 2010. Biogeography and potential exchanges among the Atlantic equatorial belt cold-seep faunas. PLoS One 5 (8), e11967.

Pawlik, J.R., 1992. Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 30, 273–335.

Pawlowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T., Gooday, A.J., 2007. Bipolar gene flow in deep-sea benthic foraminifera. Mol. Ecol. 16, 4089–4096.

Pettibone, M.H., 1976. Revision of the Genus *Macellicephala* McIntosh and the Subfamily Macellicephalinae Hartmann-Schröder (Polychaeta, Polynoidae). Smithsonian Institution Press.

Pierrot-Bults, A.C., 2008. A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. Deep-Sea Res. II 55, 137–141.

Plouviez, S., Le Guen, D., Lecompte, O., Lallier, F.H., Jollivet, D., 2010. Determining gene flow and the influence of selection across the equatorial barrier of the East Pacific Rise in the tube-dwelling polychaete *Alvinella pompejana*. BMC Evol. Biol. 10 (1), 1.

Priede, I.G., Bergstad, O.A., Miller, P.I., Vecchione, M., Gebruk, A., Falkenhaug, T., Billett, O.A., Craig, J., Dale, A.C., Shields, M.A., Tilstone, G.H., Sutton, T.T., Gooday, A.J., Inall, M.E., Jones, D.O.B., Martinez-Vincente, V., Menezes, G.M., Niedzielski, T., Sigurdsson, P., Rothe, N., Rogacheva, A., Alt, C.H.S., Brnad, T., Abell, R., Brierley, A.S., Cousins, N.J., Crockard, D., Hoelzel, A.R., Hoines, A., Letessier, T.B., Read, J.F., Shimmiels, T., Cox, M.J., Galbraith, J.K., Gordon, J.D.M., Horton, T., Neat, F., Lorance, P., 2013. Does presence of a mid-ocean ridge enhance biomass and biodiversity? PLoS One 8 (5), e61550.

Rex, M.A., Etter, R.J., 2010. Deep-sea Biodiversity: Pattern and Scale. Harvard University Press.

Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Warén, A., 2005. A source-sink hypothesis for abyssal biodiversity. Am. Nat. 165 (2), 163–178.

Rhein, M., Stramma, L., Krahmann, G., 1998. The spreading of Antarctic bottom water in the tropical Atlantic. Deep Sea Res. I 45 (4), 507–527.

Riehl, T., Brenke, N., Brix, S., Driskell, A., Kaiser, S., Brandt, A., 2014. Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. Pol. Polar Res. 35, 205–226.

Riehl, T., Riehl, L., Brandt, A., 2017. The effects of depth, distance, and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostylidae). Deep-Sea Res. II (in this issue).

Schüller, M., Ebbe, B., Wägele, J.-W., 2009. Community structure and diversity of polychaetes (Annelida) in the deep Weddell Sea (Southern Ocean) and adjacent basins. Mar. Biodivers. 39, 95–108.

Shields, M.A., Blanco-Perez, R., 2013. Polychaete abundance, biomass and diversity patterns at the Mid-Atlantic Ridge, North Atlantic Ocean. Deep Sea Res. II 98, 315–325.

Sikorski, A., Pavlova, L., 2016. Three new species of *Laonice* (Polychaete: Spionidae) from West and Southwest Africa. Zootaxa 4097 (3), 353–368.

Sikorski, A.V., 2003. *Laonice* (Polychaeta, Spionidae) in the Arctic and the North Atlantic. Sarsia 88 (5), 316–345.
Sikorski, A.V., Jirkov, I.A., Tsetlin, A.B., 1988. The genus *Laonice* (Polychaeta, Spionidae) in the Arctic Ocean, weighing the taxonomic characters and species composition. Zool. Zhurnal 67 (6), 826–838.
Thiel, D., Purschke, G., Böggemann, M., 2011. Abyssal Fauveliopsidae (Annelida) from the South East Atlantic. J. Nat. Hist. 45 (15–16), 923–937.
Tyler, P.A., Young, C.M., 1998. Temperature and pressure tolerances in dispersal stages of the genus *Echinus* (Echinodermata: echinoidea): prerequisites for deep-sea invasion and speciation. Deep Sea Res. II 45 (1), 253–277.
van Andel, T.H., Von Herzen, R.P., Phillips, J.D., 1971. The Vema fracture zone and the tectonics of transverse shear zones in oceanic crustal plates. Mar. Geophys. Res. 1 (3), 261–283.
van der Heijden, K., Petersen, J.M., Dubilier, N., Borowski, C., 2012. Genetic connectivity between north and south Mid-Atlantic ridge chemosynthetic bivalves and their symbionts. PLoS One 7 (7), e39994.
Vangriesheim, A., 1980. Antarctic bottom water flow through the Vema fracture zone. Oceanol. Acta 3 (2), 199–207.
Vanreusel, A., et al., 2010. The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. Mar. Ecol. 31, 6–20.
White, T.A., Stamford, J., Rus Hoelzel, A., 2010. Local selection and population structure in a deep-sea fish, the roundnose grenadier (*Coryphaenoides rupestris*). Mol. Ecol. 19 (2), 216–226.
Wilson, W.H., 1991. Sexual reproductive modes in polychaetes: classification and diversity. Bull. Mar. Sci. 48, 500–516.
Yearsley, J.M., Sigwart, J.D., 2011. Larval transport modelling of deep-sea invertebrates can aid the search for undiscovered populations. PLoS One 6 (8), e23063.
Young, C.M., 2003. Reproduction, development and life-history traits. In: Tyler, P.A. (Ed.), Ecosystems of the Deep Oceans. Elsevier, Amsterdam, pp. 381–426.
Young, C.M., Sewell, M.A., Tyler, P.A., Metaxas, A., 1997. Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. Biodivers. Conserv. 6, 1507–1522.
Zardus, J.D., Etter, R.J., Chase, M.R., Rex, M.A., Boyle, E.E., 2006. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). Mol. Ecol. 15, 639–651.

Author contributions

The study was designed and conducted by Theresa Guggolz.
The first draft of the manuscript and figures were prepared by Theresa Guggolz. Statistical analyses were made by Lidia Lins and Theresa Guggolz. Karin Meißner was proof-reading the manuscript and giving advice during the whole writing and review process. Angelika Brandt had the idea for the project (Vema-TRANSIT) and wrote the proposals, she was the leader of the expedition and also proof-reader of the manuscript.

CHAPTER 4

Diversity and distribution of *Laonice* species (Annelida: Spionidae) in the tropical North Atlantic and Puerto Rico Trench

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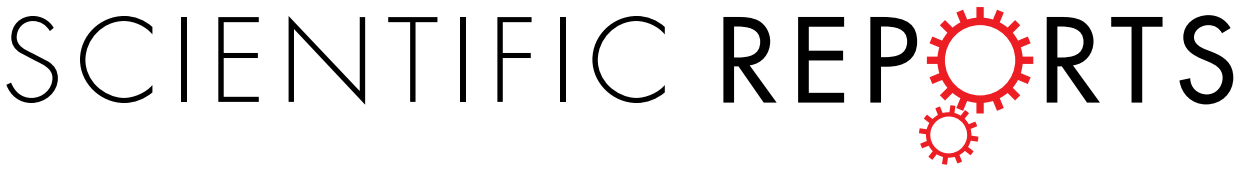

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Diversity and distribution of *Laonice* species (Annelida: Spionidae) in the tropical North Atlantic and Puerto Rico Trench

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Laonice **Malmgren, 1867 (Annelida: Spionidae) is a common polychaete genus in the deep-sea. Although most species are quite well studied morphologically, fragmentation and other damage that occurs during sampling often hampers morphological species identification of deep-sea specimens. In this study, we employ three molecular markers (16S, COI and 18S) to study the biodiversity and the distribution patterns of *Laonice* from the tropical North Atlantic and the Puerto Rico Trench. Based upon different molecular analyses (Automated Barcode Gap Discovery, pairwise genetic distances, phylogenetics, haplotype networks) we were able to identify and differentiate eight *Laonice* species. Up to four of these species co-occurred sympatrically at the same station. The majority of species were found at multiple stations and two species in the eastern as well as western Atlantic had ranges of up to 4,000 km. Genetic differentiation across these extensive geographic distances was very low. Surprisingly, one 16S haplotype was shared between individuals 2,776 km apart and individuals from the Caribbean and the abyssal plain in the eastern Atlantic (>3,389 km) differed in only a single mutation in 16S. Our results suggest that members of this genus successfully disperse across large geographic distances and are largely unaffected by topographic barriers.**

Spionidae Grube, 1850[1] is one of the most abundant and diverse groups of polychaetes and occur in almost all marine habitats, from shallow waters to the deep-sea[2]. All spionids are characterized by a pair of long palps, used for deposit or suspension feeding; most species are tube-dwellers, but free-living or commensal species are also found within the taxon[3,4]. Like several other annelid taxa, Spionidae are soft-bodied and very fragile and are, therefore, rarely found undamaged in deep-sea samples. These incomplete and fragmented individuals often lack crucial taxonomic characters, hampering their identification[5]. Nonetheless, the spionid genus *Laonice* Malmgren, 1867[6] is well studied, especially species from the deep sea of the North Atlantic[7–10]. To facilitate the identification of *Laonice* species extensive studies on species-specific characters were conducted and four subgenera were suggested based on morphological characters[8,11]. However, the recently published first molecular phylogenetic study on *Laonice* rejected two of these four subgenera[5]. Several *Laonice* species have been reported from a wide geographical range, and the presumed long planktonic life and planktotrophic larvae would offer the potential for long-distance dispersal[12–14]. However, *Laonice cirrata* (Sars, 1851[15]), a presumed widespread species, was shown to probably represent several geographically restricted species[5,16].

The abyssal Atlantic Ocean is divided by the Mid-Atlantic Ridge (MAR) longitudinally into eastern and western basins[17]. Due to its geology, the MAR is believed to represent a dispersal barrier for some components of the abyssal benthic fauna[18–21]. However, the MAR is not a closed barrier as several Fracture Zones interrupt it. When two tectonic plates passing each other in parallel to their original motions, a so-called transform fault is formed at the offsets of the ridge[22]. Over geological time the movement results in an extension past the transform fault in opposite directions, the Fracture-Zones[23].

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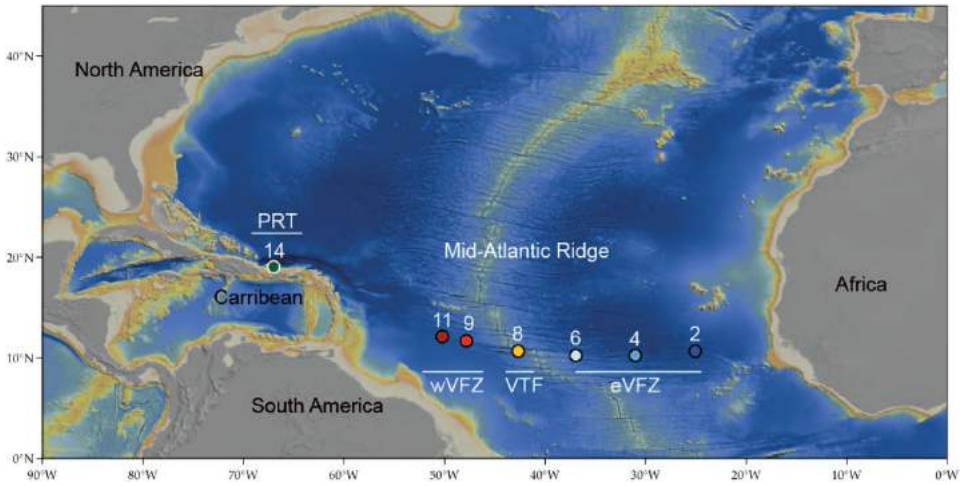

Figure 1. Map of Vema and PRT (modified after a map of N. Augustin).

Area	eVFZ			VTF	wVFZ		PRT
Site	2	4	6	8	9	11	14
2	0						
4	659	0					
6	1,298	640	0				
8	1,925	1,269	630	0			
9	2,503	1,851	1,216	589	0		
11	2,776	2,125	1,492	865	276	0	
14	4,610	3,992	3,389	2,788	2,213	1,946	0

Table 1. Distances (in km) between collection localities. Areas: eastern Vema Fracture Zone (eVFZ), western Vema-Fracture Zone (wVFZ), Vema Transform Fault (VTF), Puerto Rico Trench (PRT).

Our study area encompasses the abyssal eastern and western basins in the tropical North Atlantic along the Vema Fracture Zone as well as the Puerto Rico Trench. The first morphological studies rejected a barrier effect of the MAR on the distribution of selected widespread spionid species in the abyss of the tropical North Atlantic, though other species were found to be limited to either side of the MAR[24]. However, the presence of morphologically cryptic species could not be ruled out.

The aim of this study is to investigate the diversity and distribution of *Laonice* from the tropical North Atlantic and the Puerto Rico Trench with molecular tools and further assess the potential barrier effect of the MAR on abyssal spionid taxa.

Material and Methods

Collection and identification of specimens. All analysed specimens were collected from the tropical North Atlantic and the Puerto Rico Trench during the VEMA-Transit expedition in December 2014–January 2015 (Fig. 1, Supplement 1). Sampling was conducted with a camera-equipped epibenthic sledge at depths between 4918–5736 m, followed by a fixation of either cooled 96% ethanol or 4% buffered formalin. More detailed information about sample treatment and sampling localities are described in Guggolz *et al.*[24] and Devey *et al.*[25]. According to the geographical position, four areas were defined as following: the eastern part of the Vema-Fracture Zone (eVFZ), extending eastwards from the MAR in the Cape Verde Basin; the western part of the Vema Fracture Zone (wVFZ), extending westwards from the MAR in the Demerara Basin; the Vema Transform Fault (VTF), located between these two areas in the MAR; the Puerto Rico Trench (PRT), located in the shallower part of the trench near Puerto Rico (Fig. 1). Distances between areas varied between 276 km (wVFZ) and 1,298 km (eVFZ). The eastern-most and western-most studied sites were separated by 4,610 km (Table 1).

All specimens were sorted and identified at least to genus level using stereo zoom and compound microscopes. All specimens identified as *Laonice* and aff. *Lindaspio*[24] were analysed. The identification of the latter has been revised and reassigned to *Laonice* (unpublished data). Specimens have been deposited in the collection of the Center of Natural History (Universität Hamburg, Germany) (Supplement 1).

DNA extraction, PCR amplification, sequencing and alignment. DNA was extracted with Chelex 100. Depending on the size of specimens, one or two parapodia were dissected and transferred into 30 µl of 10% Chelex solution in purified water and incubated for 30 minutes at 56 °C and 10 minutes at 99 °C. Polymerase

Gene	Primer	Primer sequence 5′-3′	Authors
COI	jgLCO1490	TNTCNACNAAYCAYAARGAYATTGG	Geller *et al.*[65]
	jgHCO2198	TANACYTCNGGRTGNCCRAARAAYCA	Geller *et al.*[65]
	LCO1490	GGTCAACAAATCATAAAGATATTG	Folmer *et al.*[66]
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al.*[66]
	LCO2	TCNACHAAYCATAAAGAYATTGGAAC	Designed by L. Krebes and R. Bastrop
	HCOout	CCAGGTAAAATTAAAATATAAACTTC	Carpenter & Wheeler[67]
16S	16Sar	CGCCTGTTTATCAAAAACAT	Palumbi[68]
	16Sbr	CCGGTCTGAACTCAGATCACGT	Palumbi[68]
	16Sb-L	CCGGTCTGAACTCAGATCACGT	Palumbi *et al.*[69]
18S	Uni 18SF	GCTTGTCTCAGAGATTAAGCC	Dzikowski *et al.*[70]
	HET 18SR	ACGGAAACCTTGTTACGA	Dzikowski *et al.*[70]

Table 2. All Primers used in this study.

Chain Reactions (PCR) were performed with a total volume of 15 µl consisting of 1.5 µl DNA extract, 7.5 µl AccuStart II PCR ToughMix (Quanta Bio, Germany), 0.6 µl of each primer (10mmol), 0.3 µl of GelTrack loading dye (QuantaBio, Germany) and 4.8 µl Millipore H_2O. Fragments of mitochondrial (16S and COI) and nuclear (18S) rRNA genes were amplified (see Table 2 for list of all primers). PCR amplification had an initial denaturation step of 94 °C for 3 min, followed by 35 cycles of 30 s at 94 °C, 45 s at 43 °C and 45 sec at 72 °C, followed by a final elongation step for 5 min at 72 °C. Success of amplification was determined via gel electrophoresis on 1% agarose/TAE gel. For sequencing, 8 µl of the PCR products were purified using FastAP (1.6 µl; 1 U/µl) and Exonuclease I (0.8 µl; 20 U/µl) (Thermo Fisher Scientific, Germany) with an incubation time of 37 °C for 15 min followed by 15 min with 85 °C and a final holding temperature of 14 °C. Purified PCR products were sent to Macrogen Europe, Inc. (Amsterdam-Zuidoost, Netherlands) for sequencing. All in all, 80 specimens were successfully sequenced for 16S, a subset of 27 specimens for COI and 47 specimens for 18S. Sequences were assembled and corrected with Geneious 6.1.8 (http://www.geneious.com)[26] and all sequences were deposited in GenBank (for accession numbers see Supplement 1). The obtained sequences of the different gene fragments were aligned separately using MUSCLE[27] implemented in Genious 6.1.8.

Initial identification of species, phylogenetic analyses and haplotype networks. To obtain a first estimation of the number of species among *Laonice* investigated, the Automated Barcode Gap Discovery (ABGD[28]) was conducted separately for each of the three genes (16S, COI, 18S). The ABGD identifies potential barcoding gaps separating hypothetical species, based on the assumption that interspecific genetic distances are larger than intraspecific distances. The ABGD analysis was run on the web-based version of the software (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html), using uncorrected p distances (Table 3), which were calculated with MEGA7[29] on all available sequences. Standard settings were kept, except for Pmin (0.005), the numbers of steps (100) and the relative gap width (X = 0.5).

To assess the phylogenetic relationships among the studied specimens and to assess whether the lineages suggested by ABGD are monophyletic, phylogenetic analyses were performed with Bayesian inference. All three gene fragments were analysed separately and concatenated with MrBayes (version 3.2[30]) online with CIPRES Science Gateway V.3.3 (www.phylo.org)[31]. For the analyses of the 16S and COI genes, *Marenzelleria neglecta* Sikorski & Bick, 2004[32], *Malacoceros indicus* (Fauvel, 1928)[33], *Polydora hoplura* Claparède, 1868[34] and *Spio blakei* Maciolek, 1990[35] were employed as outgroups (Supplement 2). Four chains were run for 10^7 generations, with sampling every 1200th generation, and discarding the first 25% as burn-in. The GTR + I + G substitution model was identified by MEGA7 as the best fitting model under the AIC criterion.

Guggolz *et al.*[24] studied the same *Laonice* individuals morphologically. That data was used to identify morphological differences between the herein delimited species and to add another line of evidence for species delimitation.

To assess the genus-wide phylogenetic relationships of the herein studied *Laonice* and to find out whether any of these species have a wider distribution than anticipated by our own data, a phylogenetic analysis with *Laonice* sequences available from GenBank was conducted for COI and 16S. Additional data includes: *Laonice* from expeditions around Iceland (IceAGE I + II[5]) and other GenBank entries[14,36–43] (Supplement 2). The genus-wide analysis was focussed on the COI data, because of the more comprehensive COI data being available (Supplement 2), even if analysis with 16S data was also conducted (Supplement 3).

To better visualize the geographic distribution of the genetic diversity median-joining haplotype networks were generated with Network 5.0.0.3[44] (http://fluxus-engineering.com/) for each gene fragment. The generated haplotype networks were redrawn with Adobe Illustrator CS6.

Analyses of population differentiation were performed with Arlequin 3.5[45] for species with sufficiently large specimen numbers (at least four specimens per site). Pairwise Φst was calculated for *Laonice* sp. D, F, H (16S). For *Laonice* sp. D areas eVFZ and wVFZ, for *Laonice* sp. F areas eVFZ and VTF and for *Laonice* sp. H the areas eVFZ, wVFZ and VTF were compared (Tables 4 and 5).

	Laonice sp. A	*Laonice* sp. B	*Laonice* sp. C	*Laonice* sp. D	*Laonice* sp. E	*Laonice* sp. F	*Laonice* sp. G	*Laonice* sp. H
Laonice sp. A	0 X 0.1							16S COI 18S
Laonice sp. B	18.7–19.9 21.9 0.9–1.3	0.4 0.0 0.3						
Laonice sp. C	16.2 23.0 0.7–0.8	10.7 17.4 0.3–0.6	X X X					
Laonice sp. D	17.0–23.0 21.7–22.6 1.9–2.1	16.1–20.4 20.3–20.7 1.4–1.8	15.8–21.4 20.2–20.7 1.3	0.0–1.4 0.0–0.7 0.0				
Laonice sp. E	17.2 X 2.0–2.1	14.8–15.3 X 1.4–1.8	14.7 X 1.3	6.3–8.2 X 0.1	X X X			
Laonice sp. F	17.5–19.4 23.0 1.8–1.9	14.8–17.0 20.4–20.5 1.3–1.6	15.0–17.3 20.2 1.2	8.2–12.7 14.0–14.8 0.1–0.2	7.1–8.2 X 0.2	0.0–1.7 X 0.0		
Laonice sp. G	18.5–21.9 21.9–22.0 1.8–1.9	15.3–17.1 20.2–20.7 1.3–1.6	15.1–15.5 20.5–20.7 1.2	8.2–10.8 15.3–15.9 0.1–0.2	4.7–5.1 X 0.2	2.8–4.0 8.6–8.8 0.0	0.0–0.2 0.5 0.0	
Laonice sp. H	18.5–19.7 22.3–22.7 2.0–2.8	15.8–16.4 22.4–22.9 1.5–2.5	15.4–17.1 20.7–21.0 1.4–2.1	4.1–8.2 11.7–12.4 0.1–0.9	7.1–8.2 X 0.2–0.7	10.9–13.2 17.0–17.5 0.2–0.9	6.4–7.3 14.2 –14.9 0.2–0.9	0.0–1.0 0.2–0.7 0.0

Table 3. Percentage of uncorrected p-distances within and among lineages for COI, 16S and 18S (see upper right corner). "X" means no or only one sequence available.

	site	No. of ind.	No. of haplotypes	Nucleotide diversity ± SD	Tajima's D (p-value)	Fu's F_s (p-value)
***Laonice* sp. D**						
eVFZ	2	18	5	0.0035 ± 0.0027	−0.465 (0.601)	−0.679 (0.2630)
	4	8	6			
	6	4	1			
wVFZ	9	3	2	0.0018 ± 0.0023		
***Laonice* sp. F**						
eVFZ	2	5	5	0.0084 ± 0.0055	−1.174 (0.089)	−1.205 (0.098)
	4	3	3			
VTF	8	5	5	0.00187 ± 0.0019		
***Laonice* sp. H**						
eVFZ	6	3	3	0.0025 ± 0.0022	−0.333 (0.465)	0.261 (0.425)
VTF	8	3	6	0.0021 ± 0.0020		
wVFZ	9	2	4	0.0024 ± 0.0024		

Table 4. Population indices for 16S of selected *Laonice* species among sites and geographic areas. Nucleotide diversity, Tajima's D and Fu's Fs are reported only for the areas, not the individual sites. (eVFZ: eastern Vema Fracture Zone, wVFZ: western Vema-Fracture Zone, VTF: Vema Transform Fault).

Results

Alignment. The alignment of the 16S fragment included a total of 79 sequences with a length of 525 bp, of which 223 bp were variable and 165 bp were parsimony informative. The COI alignment featured 26 sequences and had a length of 694 bp, of which 283 bp were variable and 207 bp parsimony informative. The alignment contained no indels and the derived amino acid alignment consisted of 208 amino acids, with 16 variable amino acids and no stop codons. The genus-wide COI alignment featured 134 sequences (including outgroup) and had a length of 683 bp, of which 324 were variable and 301 were parsimony informative. The alignment of the 18S fragment consisted of 46 sequences with 2195 bp, of which only 68 bp were variable and 34 bp were parsimony informative.

Species delimitation. The ABGD analysis of the 16S dataset retrieved eight main lineages when barcode thresholds of 0.5–4.5% were employed. For now, we use the term lineages rather than species, as not all of them necessarily correspond to species. To the eight lineages, we will refer to as *Laonice* sp. A–H. With higher threshold values several lineages collapsed (4.6–6.5% = 3 lineages), or all lineages collapsed into a single lineage (>6.7%). The analysis of the COI dataset resulted in seven lineages (barcode thresholds 0.5–10%). The seven lineages identified with COI are in full agreement with the lineages derived with 16S, with the same specimens being clustered

***Laonice* sp. D**	**eVFZ site 2**	**site 4**	**site 6**	**wVFZ site 9**
site 2	0.000			
site 4	0.000	0.000		
site 6	0.175	0.111	0.000	
site 9	0.000	0.000	0.015	0.000
***Laonice* sp. F**	**eVFZ site 2**	**eVFZ site 4**	**VTF site 8**	
site 2	0.000			
site 4	0.000	0.000		
site 8	0.000	0.008	0.000	
***Laonice* sp. H**	**eVFZ site 6**	**VTF site 8**	**wVFZ site 9**	
site 6	0.000			
site 8	0.000	0.000		
site 9	0.000	0.000	0.000	

Table 5. Pairwise Φst values among different sites for 16S of selected *Laonice* species among sites. (eVFZ: eastern Vema Fracture Zone, wVFZ: western Vema-Fracture Zone, VTF: Vema Transform Fault).

together. The discrepancy between 16S and COI is due to the absence of one lineage, *Laonice* sp. E (PVT 471_I), which was not successfully sequenced for COI. Pairwise genetic distances (uncorrected *p*-distances) between the lineages ranged for 16S from 2.8–23%, for COI from 8.6–23% and for 18S from 0–2.8% (based on the eight lineages derived by 16S) (Table 3). The lowest pairwise distances were found between the lineages F and G (16S: 2.8–4%; COI: 8.6–8.8%; 18S: 0%), whereas all other pairwise distances between the lineages were higher than 4.1% for 16S, 12.2% for COI and 0.1% for 18S. Within lineages, the highest observed pairwise distances were 1.7% for 16S, 0.7% for COI and 0.3% for 18S (Table 3).

The phylogenetic analyses of COI and 16S recovered lineages A-H as reciprocal monophyletic with full support each (Fig. 2). Also the phylogenetic relationships among the lineages were very similar for 16S and COI. *Laonice* sp. F and G are sister species (in 16S, *Laonice* sp. E clusters with these two species), as are *Laonice* sp. C and B as well as *Laonice* sp. D and H. Differences between the analyses of the 16S and COI data are found in the position of *Laonice* sp. A. In COI, *Laonice* sp. A is found to be a sister taxon to *Laonice* sp. B and C (Fig. 2a), whereas in 16S *Laonice* sp. A is placed as a sister taxa to all other species (Fig. 2b).

The haplotypes networks of the different gene fragments (16S, COI and 18S) showed slightly different patterns (Fig. 3a–c). For 16S, with the highest number of sequenced individuals, 27 haplotypes (h1-16S-h27-16S) were found with a maximum of eight haplotypes in one lineage (*Laonice* sp. D, Fig. 3a). Networks of COI dataset showed a total of 18 different haplotypes (h1-COI–h18-COI) with a maximum of six haplotypes within the same lineage as in 16S (*Laonice* sp. D, Fig. 4b). For 18S the smallest genetic diversity was found with 17 haplotypes (h1-18S–h17-18S; Fig. 3c). The low number of mutational steps between haplotypes, as evidenced in the 18S network (Fig. 3c), is probably responsible for the lower resolution in the phylogenetic analysis of this gene when it comes to species delimitation. The 18S network shows that *Laonice* sp. A, B and C are well differentiated from each other and the other lineages. *Laonice* sp. D, E, F, G and H all have very similar haplotypes and do not form well differentiated clusters. *Laonice* sp. F and G even share their only haplotype.

As all investigated specimens were incomplete or damaged and relatively short (maximum 22 segments), the main characters for species identification were the shape of the prostomium, the beginning of the lateral pouches, the beginning of the sabre chaeta and the beginning and number of teeth of the neuropodial hooks, as well as the length of the nuchal organ (Table 6).

Slight morphological variations were observed between the eight species delimitated with molecular analyses. For instance, *Laonice* sp. F and sp. G differ in the beginning of the lateral pouches (sp. F: 3rd chaetiger; sp. G: 4th chaetiger), the beginning of the sabre chaeta (sp. F: 10th chaetiger; sp. G: 8th chaetiger) as well as the length of the nuchal organ (sp. F: until 9th chaetiger; sp. G: until 8th chaetiger) (Table 6). Furthermore, *Laonice* sp. B was the only species with the peri- and prostomium fused and in *Laonice* sp. E the beginning of the neuropodial hooks was observed more posteriorly than in all other species (16th chaetiger). *Laonice* sp. A differed from all other species, as the nuchal organ reached the end of the available fragments (until 18th chaetiger) and a prominent dorsolateral ridge was present from chaetiger 8 —11 (Table 6).

Distribution of species. In the genus-wide phylogenetic analysis of COI with *Laonice* species from the Atlantic, the Southern Ocean, Russian waters and the North-East Pacific, all *Laonice* lineages identified herein were recovered as monophyletic, and none of these seemed to be conspecific with any of the published *Laonice* sequences (Fig. 4). *Laonice* sp. D, F, G and H constitute a monophylum, within a clade including *Laonice blakei* Sikorski and Jirkov in Sikorski *et al.*[46] and *Laonice* sp. b sensu Bogantes *et al.*[5], both sampled from Icelandic waters. *Laonice* sp. B and C constitute a monophyletic group that is sister to a large clade of *Laonice* species, including *Laonice* sp. A, from various localities (Fig. 4).

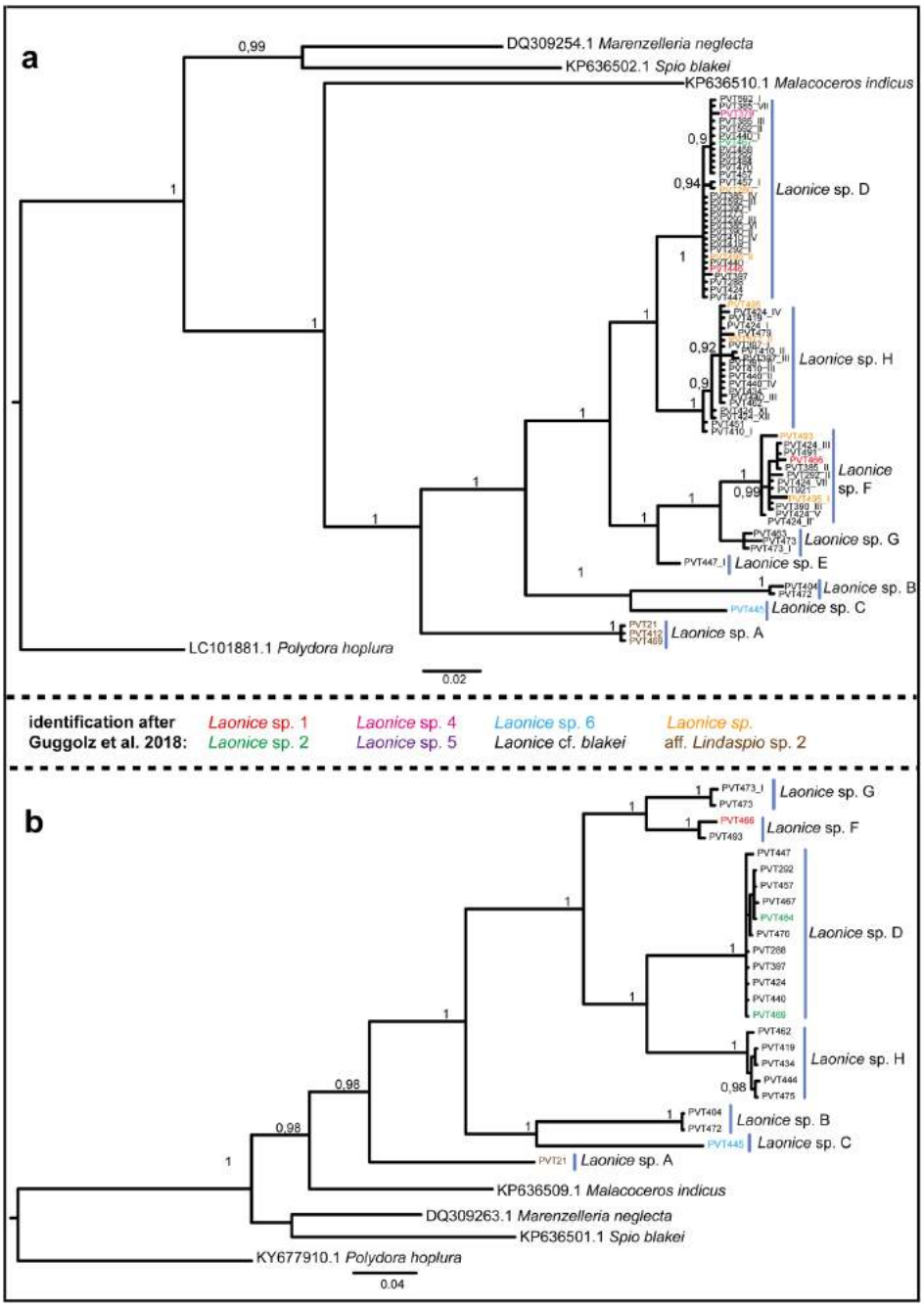

Figure 2. Phylogenetic tree of Laonice specimens from the Vema-Transit expedition based on mitochondrial 16S (**a**) and COI (**b**) gene fragments. Posterior probabilities shown next to the nodes (values below 0.8 are not shown). Morphological identification after Guggolz *et al.* 2018[24] are color coded (see legend in the middle).

Five of the lineages were only recorded in one of the four areas: *Laonice* sp. A and B in the eVFZ, *Laonice* sp. C and E in the wVFZ and *Laonice* sp. G in the PRT (Fig. 3). These five lineages were relatively rarely collected with three specimens at most (Supplement 1). In contrast, the other three lineages were recorded at larger geographic scales, in either the eVFZ and VTF (*Laonice* sp. F) or even in all four areas (*Laonice* sp. D and H). Even single haplotypes of these lineages exhibited such extensive distributions and were recorded in all of these areas, except PRT (16S: h5, h7, h15, h17, h23; COI: h5, h15; 18S: h7, h13, h14, h15; Fig. 3). For example, *Laonice* sp. D had one haplotype in each of the three studied genes that occurred in the eVFZ, VTF as well as the wVFZ (Fig. 3: h7-16S, h5-COI, h7-18S).

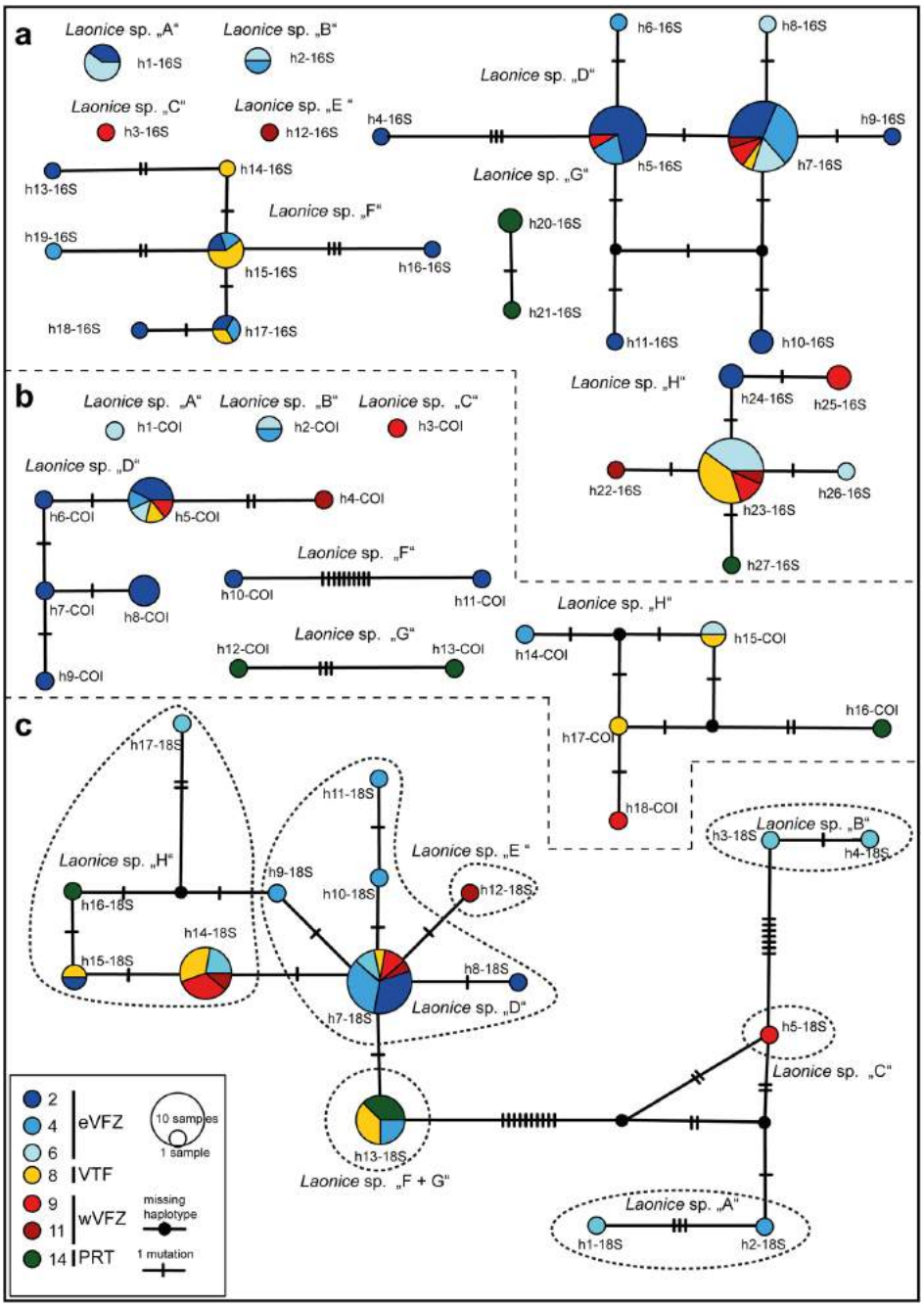

Figure 3. Haplotype networks of Laonice species from the Vema-Transit expedition of 16S (**a**), COI (**b**) and 18S (**c**) gene fragments.

Population differentiation was not significant, neither between different sites, nor between different areas for the three widely distributed lineages *Laonice* sp. D, F and H (Tables 4 and 5).

Discussion

Employing mitochondrial markers (16S and COI) we were able to identify eight lineages well supported and consistently delimited. Following a strict DNA barcoding approach (*sensu* Hebert *et al.*[47]), these results might easily be interpreted as eight species. However, mitochondrial markers are linked and thus not independently inherited. Therefore, consistency among these markers does not necessarily equate reproductive isolation among

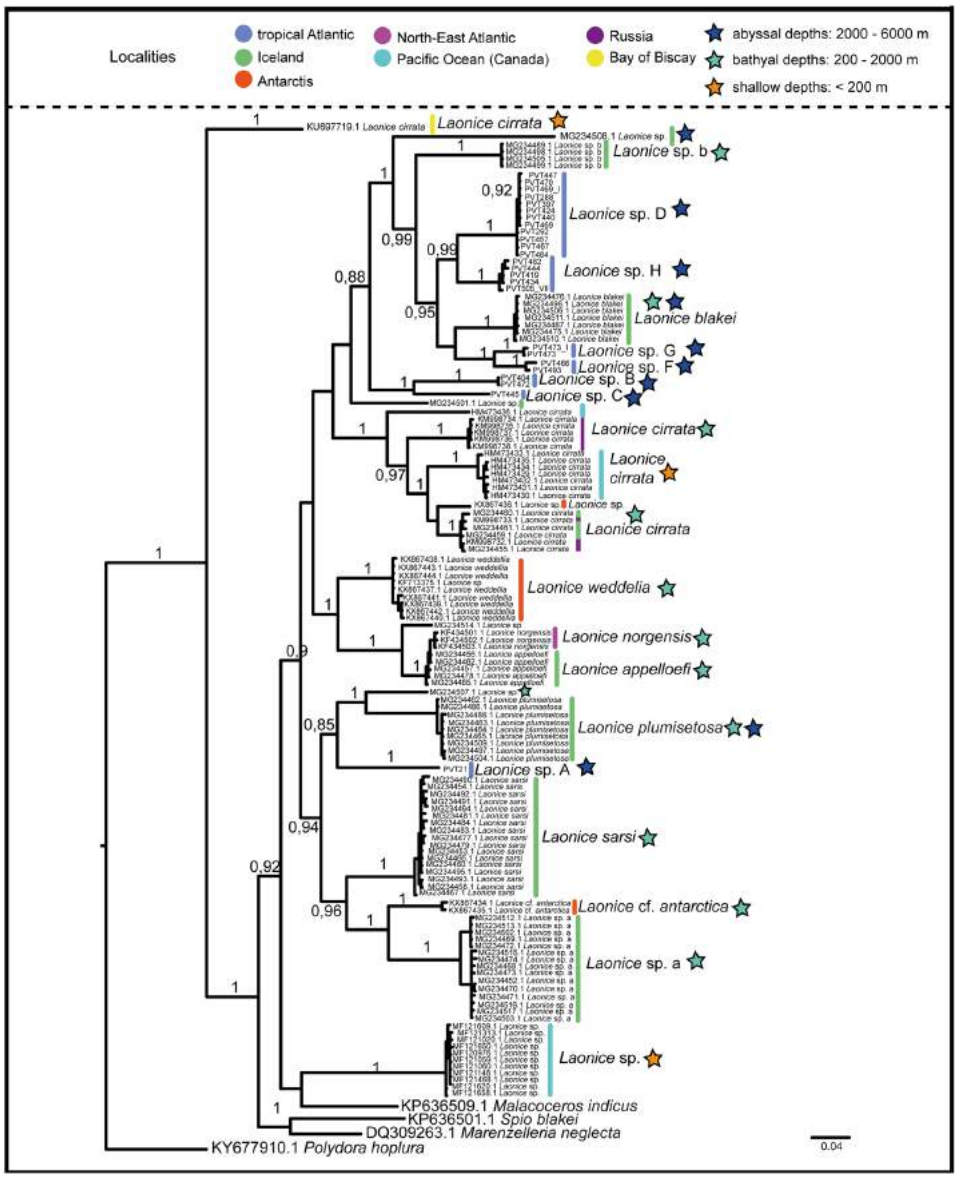

Figure 4. Phylogenetic tree of Laonice specimens from the Atlantic, Antarctic and Pacific Ocean based on the mitochondrial COI gene fragment. Posterior probabilities shown next to the nodes (values below 0.8 are not shown). Sampling localities and depth are colour coded (see legend in upper right-hand corner).

the respective lineages[48]. Consistency with other marker types - e.g., nuclear markers or morphology - does offer the possibility to delimit species adequately[49,50]. Taken all data together, lineages A, B, C, D, E and H can be easily delimited as distinct species, even though the differentiation is less pronounced between lineages D, E and H in 18S. The lack of shared haplotypes, despite their sympatric distribution over large geographic scales, is a good indication of reproductive isolation among them. Lineages F and G shared an identical 18S haplotype and also their pairwise uncorrected distances were the lowest for all pairs of lineages (COI: 8.6–8.8%; 16S: 2.8–4.0%). However, a lack of differentiation in 18S may not be surprising for recently diverged species and the levels of differentiation in COI and 16S are comparable to those observed among other polychaete species, which usually exceeded 5–6% for COI[51–54]. Intraspecific distances were always lower than interspecific distances with a maximum of 1.7% within *Laonice* sp. F for 16S and 0.7% within *Laonice* sp. H for COI (Table 3), similar to the 0–2% uncorrected distances found within *Laonice* species from the North-Atlantic[5]. These results could imply thresholds of about 2% for 16S and 2–8% for COI to distinguish between *Laonice* species.

Species name	No. of spec. characters observed	Nuchal organ end	Start Neuropodial hooks/number of teeth	Lateral pouches start	Sabre chaeta start	Remarks
Laonice sp. A	2	end of fragment; 18th chaetiger	9th chaetiger	no pouches seen		prominent dorsolateral ridge 8–11th
Laonice sp. B	2	??	??	3rd chaetiger		Peri- und Prostomium fused; very short; 2nd and 3rd branchia different shape than *L.* cf. *blakei*, triangular
Laonice sp. C	1	9th chaetiger	??	??	11th chaetiger	Pro-und peristomium not fused; 3–4 rows of cappillaries
Laonice sp. D	10	8th – 10th chaetiger	13–15th chaetiger/5 teeth in side view	3rd chaetiger	9th - 11th	no eyes; occipital antennae prominent; Pro-and Peristomium not fused; 3–4 rows of capillaries
Laonice sp. E	1	??	16th chaetiger	3rd chaetiger	??	2 rows of capillaries; very short
Laonice sp. F	3	9th chaetiger	9th - 10th chaetiger	3rd chaetiger	10th chaetiger	
Laonice sp. G	2	8th chaetiger	??	4th chaetiger	8th chaetiger	
Laonice sp. H	4	10th chaetiger	14th/15th chaetiger	3rd chaetiger	11th chaetiger	

Table 6. Morphological differences (investigated by Guggolz *et al.* 2018[24]) of the eight *Laonice* species (*Laonice* A–G). Question marks are used, if material was insufficient to see characters, respectively.

The present molecular study reveals inconsistencies with previous morphology based studies[24]. Guggolz *et al.*[24] identified six species (aff. *Lindaspio* sp. 1, *Laonice* sp. 1, 4, 5, 6 and *Laonice* cf. *blakei*). The majority of specimens were identified as *L.* cf. *blakei* (about 86.5% of the identified *Laonice* specimens) and the slight variations observed between individuals were interpreted as intraspecific variability within *L.* cf. *blakei*. Of the six species identified based on their morphology by Guggolz *et al.*[24], only *Laonice* sp. A (aff. *Lindaspio* sp. 1 in Guggolz *et al.*[24]) and sp. C (*Laonice* sp. 6 in Guggolz *et al.*[24]) could be confirmed in our molecular analyses. Specimens identified as *Laonice* cf. *blakei* by Guggolz *et al.*[24] are here assigned to six different species based on the results from molecular studies: *Laonice* sp. B, D, E, F, G and H. Furthermore, *Laonice* sp. 2, 4, and 5 are all included in *Laonice* sp. D and *Laonice* sp. 1 included in *Laonice* sp. F (see Fig. 2). Most of the disagreement between the morphological study and the present results can be explained as misinterpretations of morphological differences as intraspecific variability rather than interspecific variation. The slight differences observed among individuals identified as *Laonice* cf. *blakei* probably represent interspecific variation between several species of *Laonice*. Taken together with the molecular data, these variations lend additional support for differentiating the eight species identified herein. For instance, *Laonice* sp. F and sp. G, sharing the same 18S haplotype, showed differences in their morphology, supporting a separation at the species level. Comparable morphological differences can be found for *Laonice* sp. A–E as well.

These morphological patterns support the differentiation of the eight lineages and we therefore propose that these eight lineages represent eight species. The lack of differentiation in 18S is probably caused by a combination of a low substitution rate and incomplete lineage sorting[55] rather than ongoing reproduction among these species.

Apart from delimiting species, we were interested in distribution patterns of the species. Even over large geographic distances (>4,000 km; Table 1, Fig. 3), there seems to be no genetic differentiation within some species. This is most obvious for species distributed across the MAR (*Laonice* sp. D, H), as the same haplotypes are found in the eVFZ and the wVFZ. Species restricted to only one (*Laonice* sp. A and B in the eVFZ) or two of the areas (*Laonice* sp. F in the eVFZ and the VTF) exhibited identical haplotypes across distances of hundreds of kilometres. These species might represent rare species and we could have missed them in the other areas due to the sampling design, as we managed to obtain a higher number of individuals from the eVFZ compared to the other sampled areas[24,25] (Supplement 1). The present data suggest gene flow over the MAR or potentially through Fracture Zones in the tropical North Atlantic, supported by the low and non-significant levels of differentiation among populations (*Laonice* sp. D, F and H). Guggolz *et al.*[24] already suggested that the Mid-Atlantic Ridge (MAR) does not represent a physical barrier for some polychaetes based on morphological studies and the lack of significant differences between the eastern and western sides of the ridge. A widespread distribution over 4,000 km was never proven genetically for *Laonice*, but it was reported for other abyssal taxa like *Aurospio dibranchiata* Maciolek, 1981[56], a polychaete species occurring in different oceans[37] and *Nicomache lokii* Kongsrud & Rapp, 2012[57] and *Sclerolinum contortum* Smirnov, 2000[58], polychaetes living in chemosynthetic-based ecosystems distributed from the Arctic to Antarctic[59]. Larval distribution is suggested to play a major role in the efficiency of the distribution of deep-sea invertebrates, even if the specific larvae are unknown for most species[60]. The exact types of development of the investigated *Laonice* specimens from the tropical North Atlantic is unknown, but in general *Laonice* is supposed to have long-lived larvae and very high dispersal capabilities[12,14,24]. The development strategies seem to be highly connected with the ability to distribute in the abyss even with potential topographic barriers like ridges, rises or canyons. For instance, different molluscs with planktonic larvae were reported to be

able to distribute over such barriers[61,62]. Contrary, taxa with direct development, such as brooding isopods, were found to have a restricted distribution with limited or no gene flow across the MAR[18,63].

None of the eight species recorded in the tropical North Atlantic were found to be conspecific with *Laonice* species for which published genetic data was available. Bogantes *et al.*[5] recently performed first phylogenetic studies on *Laonice* and suggested that the Antarctic was colonized several times independently. A comparable pattern can be found in our study. Nonetheless, one should keep in mind that these results are based only on one gene (COI) and only a small proportion of known *Laonice* species are included.

Until now, around 16 deep-sea *Laonice* species have been described, mainly based on morphology[9]. Unfortunately, it is not possible to perform subsequent molecular studies with most of the described material, due to fixation, unless new material is collected from the respective type localities. Identification of *Laonice* specimens from deep-sea samples is almost always difficult due to fragmentation and the subsequent loss of important characters independently of the fixation method[5,24]. Therefore, molecular techniques might be of great importance for a correct estimation of their diversity. DNA extraction from fresh material before fixation in formalin takes place would be an appropriate way to combine morphology and molecular studies in soft-bodied animals like spionid polychaetes and should be part of the workflow during sampling.

The present study gives new insights into the phylogeny of *Laonice* and stresses the importance of molecular analyses for estimates of species diversity, ideally combined with morphological studies. The eight *Laonice* species identified in the tropical North Atlantic might be new to science, and certainly do not belong to any of the *Laonice* species investigated with molecular tools to date. Due to the incomplete specimens and thus the absence of important morphological characters, a clear differentiation from all described *Laonice* species is impossible. Therefore, at present the identified lineages cannot be described as new species. However, molecular data is sparse for the genus and new information would further improve our understanding of the evolution of *Laonice* and the dynamics of speciation in the deep-sea. Our present study highlights the importance of integrative taxonomy to allow species delimitation in deep-sea spionids.

The genus' potential to disperse over large geographic distances in the deep-sea and across topographic barriers such as ridges is shown here and support the hypothesis of other studies[14,64]. We were able to show the occurrence of the same *Laonice* species from the Caribbean to the abyssal plain near West-Africa, highlighting for the first time such a wide distribution for a species of this genus based on molecular analyses. These dispersal abilities are also notable for annelids in general, showing the relevance of molecular tools for our understanding of their distribution in the deep-sea.

References

1. Grube, A. E. Die Familien der Anneliden. *Archiv für Naturgeschichte.* **16**, 249–364 (1850).
2. Blake, J. A., Maciolek, N. J. & Meißner, K. Spionidae Grube, 1850 in *Handbook of Zoology*, *a Natural History of the Phyla of the Animal Kingdom—Annelida*, *Polychaetes* (ed. Schmidt-Rhaesa, A.) 1–109 (De Gruyter, 2017).
3. Glasby, C. J. *et al*. Class polychaeta in *Polychaetes & Allies: The Southern Synthesis. Fauna of* Australia (eds Beesley, P. L., Ross, B., Glasby, C. J.) 1–296 (Melbourne: CSIRO Publishing 2000).
4. Jumars, P. A., Dorgan, K. M. & Lindsay, S. M. Diet of worms emended: an update of polychaete feeding guilds. *Annu. Rev. Mar. Sci.* **7**, 497–520 (2015).
5. Bogantes, V. E., Halanych, K. M. & Meißner, K. Diversity and phylogenetic relationships of North Atlantic *Laonice* Malmgren, 1867 (Spionidae, Annelida) including the description of a novel species. *Mar. Biodivers*, 1–13 (2018).
6. Malmgren, A. J. Annulata Polychaeta Spetsbergiæ, Groenlandiæ, Islandiæ et Scandinaviæ. Hactenus Cognita. *Ex Officina Frenckelliana, Helsingforslæ*. **127** (1867).
7. Maciolek, N. J. New species and records of *Aonidella*, *Laonice*, and *Spiophanes* (Polychaeta: Spionidae) from shelf and slope depths of the Western North. *Atlantic. B. Mar. Sci.* **67**, 529–548 (2000).
8. Sikorski, A. V. *Laonice* (Polychaeta, Spionidae) in the Arctic and the North Atlantic. *Sarsia* **88**, 316–345 (2003).
9. Sikorski, A. V., Gunton, L. M. & Pavlova, L. *Laonice* species (Polychaeta, Spionidae) from the Whittard Canyon (NE Atlantic) with descriptions of two new species. *J. Mar. Biol. Assoc. U. K.* **97**, 961–973 (2017).
10. Sikorski, A. V. & Pavlova, L. Three new species of *Laonice* (Polychaete: Spionidae) from West and Southwest Africa. *Zootaxa* **4097**, 353–368 (2016).
11. Sikorski, A. V. Review of *Laonice* (Spionidae, Annelida) with remarks on several species and a description of a new species from South Africa. *Ital. J. Zool.* **78**, 37–41 (2011).
12. Blake, J. A. Spionida in *Reproductive biology and phylogeny of* Annelida (eds Rouse, G. and Pleijel, F.) 565–638 (Science Publishers, Enfield 2006).
13. Wilson, W. H. Sexual reproductive modes in polychaetes: classification and diversity. *B- Mar. Sci.* **48**, 500–516 (1991).
14. Meißner, K., Bick, A., Guggolz, T. & Götting, M. Spionidae (Polychaeta: Canalipalpata: Spionida) from seamounts in the NE Atlantic. *Zootaxa* **3786**, 201–245 (2014).
15. Sars, M. Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken [1850 date used in Hydrozoa, 1851 in Polychaeta & others]. *Nyt Magazin for Naturvidenskaberne* **6**, 121–211 (1851).
16. Sikorski, A. V. On distinguishing of *Laonice cirrata* (Sars, 1851) and *Laonice bahusiensis* Söderström, 1920 (Polychaeta: Spionidae) – the two morphologically related species. *Zool Zhurnal* **81**(4), 406–419 (2002).
17. Murray, J. & Hjort, J. The Depths of the Ocean. (McMillan, London 1912).
18. Bober, S., Brix, S., Riehl, T., Schwentner, M., Brandt, A. Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean? *Deep-Sea Res. Pt II* **148**, 91-104 (2018).
19. Brandt, A. *et al*. Composition of abyssal macrofauna along the Vema Fracture Zone and the hadal Puerto Rico Trench, northern tropical Atlantic. *Deep-Sea Res. Pt II* **148**, 35-44 (2018).
20. McClain, C. R., Rex, M. A. & Etter, R. J. Deep-sea macroecology in *Marine* Macroecology (eds. Witman, J. D., Roy, K.) 65–100 (Chicago, IL: University of Chicago Press 2009).
21. Priede, I. G. *et al*. Does presence of a mid-ocean ridge enhance biomass and biodiversity? *PLoS One* **8**(5), e61550 (2013).
22. Ball, M. M. & Harrison, C. A. Crustal plates in the central Atlantic. *Science* **167**(3921), 1128–1129 (1970).
23. van Andel, T. H., von Herzen, R. P. & Phillips, J. D. The Vema fracture zone and the tectonics of transverse shear zones in oceanic crustal plates. *Mar. Geophys. Res.* **1**(3), 261–283 (1971).
24. Guggolz, T., Lins, L., Meißner, K. & Brandt, A. Biodiversity and distribution of polynoid and spionid polychaetes (Annelida) in the Vema Fracture Zone, tropical North Atlantic. *Deep-Sea Res. Pt II* **148**, 54–63 (2018).

25. Devey, C. W. RV SONNE Fahrtbericht/Cruise Report SO237 Vema-TRANSIT: bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study, Las Palmas (Spain)-Santo Domingo (Dom. Rep.) 14.12.14–26.01.15 (2015).
26. Kearse, M. *et al*. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28.12**, 1647–1649 (2012).
27. Edgar, R. C. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* **32**, 1792–1797 (2004).
28. Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Mol. Ecol.* **21**(8), 1864–1877 (2012).
29. Kumar, S., Stecher, G. & Tamura, K. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Mol. Biol. Evol.* **33**, 1870–1874 (2016).
30. Ronquist, F. & Huelsenbeck, J. P. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**(12), 1572–1574 (2003).
31. Miller, M. A., Pfeiffer, W. & Schwartz, T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees in *Proceedings of the Gateway Computing Environments Workshop* (*GCE*) 1–8. (New Orleans, LA 2010).
32. Sikorski, A. V. & Bick, A. Revision of *Marenzelleria* Mesnil, 1896 (Spionidae, Polychaeta). *Sarsia* **89**(4), 253–275 (2004).
33. Fauvel, P. Annélides Polychètes nouvelles de l'Inde in *I. Bulletin du Muséum d'Histoire Naturelle*, **34**(**1**), 90–96 (Paris, 1928).
34. Claparède, É. Les annélides chétopodes du Golfe de Naples. *Mémoires de la Société de physique et d'histoire naturelle de Genève* **19**, 313–584 (1868).
35. Maciolek, N. J. A. redescription of some species belonging to the genus *Spio* and *Microspio* (Polychaeta: Annelida) and descriptions of three new species from Northwestern Atlantic Ocean. *J. Nat. Hist.* **24**, 1109–1141 (1990).
36. Bastrop, R. & Blank, M. Multiple invasions–a polychaete genus enters the Baltic Sea. *Biol. Invasions* **8**(5), 1195–1200 (2006).
37. Mincks, S. L., Dyal, P. L., Paterson, G. L. J., Smith, C. R. & Glover, A. G. A new species of Aurospio (Polychaeta, Spionidae) from the Antarctic shelf, with analysis of its ecology, reproductive biology and evolutionary history. *Mar. Ecol.* **30**, 181–197 (2009).
38. Brasier, M. J. *et al*. Distributional Patterns of Polychaetes across the West Antarctic Based on DNA Barcoding and Particle Tracking. Analyses. *Front. Mar. Sci.* **4**, 356 (2017).
39. Carr, C. M., Hardy, S. M., Brown, T. M., Macdonald, T. A. & Hebert, P. D. N. A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian Polychaetes. *PLoS One* (2011).
40. Gallegos, R., Lavery, S. & Sewell, M. A. The meroplankton community of the oceanic Ross Sea during late summer. *Antarc. Sci.* **26**(4), 345–360 (2014).
41. Williams, L.-G., Karl, S. A., Rice, S. & Simon, C. Molecular identification of polydorid polychaetes (Annelida: Spionidae): is there a quick way to identify pest and alien species? *Afr. Zool.* **52**(2), 105–117 (2017).
42. Sato-Okoshi, W., Abe, H., Nishitani, G. & Simon, C. A. And then there was one: Polydora uncinata and Polydora hoplura (Annelida: Spionidae), the problematic polydorid pest species represent a single species. *J. Mar. Biol. Assoc. U. K.* **97**(8), 1675–1684 (2017).
43. Meißner, K. & Götting, M. Spionidae (Annelida:'Polychaeta': Canalipalpata) from Lizard Island, Great Barrier Reef, Australia: the genera *Malacoceros*, *Scolelepis*, *Spio*, *Microspio*, and *Spiophanes*. *Zootaxa* **4019**(1), 378–413 (2015).
44. Bandelt, H. J., Forster, P. & Röhl, A. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **16**(1), 37–48 (1999).
45. Excoffier, L. & Lischer, H. E. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**(3), 564–567 (2010).
46. Sikorski, A. V., Jirkov, I. A. & Tsetlin, A. B. The genus *Laonice* (Polychaeta, Spionidae) in the Arctic Ocean: weighing the taxonomic characters and species composition. *Zool Zhurnal* **67**, 826–838 (1988).
47. Hebert, P. D., Ratnasingham, S. & de Waard, J. R. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proc. Royal Soc. B* **270**, 96–99 (2003).
48. Ballard, J. W. O. & Whitlock, M. C. The incomplete natural history of mitochondria. *Molec. Ecol.* **13**(4), 729–744 (2004).
49. Schwentner, M., Timms, B. V. & Richter, S. An integrative approach to species delineation incorporating different species concepts: a case study of *Limnadopsis* (Branchiopoda: Spinicaudata). *Biol. J. Linn. Soc.* **104**, 575–599 (2011).
50. Schwentner, M., Just, F. & Richter, S. Evolutionary systematics of the Australian Cyzicidae (Crustacea, Branchiopoda, Spinicaudata) with the description of a new genus. *Zool. J. Linn. Soc.* **173**, 271–295 (2014).
51. Kvist, S. Does a global DNA barcoding gap exist in Annelida? *Mitochond. DNA Pt A* **27**(3), 2241–2252 (2016).
52. Janssen, A. *et al*. reverse taxonomic approach to assess macrofaunal distribution patterns in abyssal pacific polymetallic nodule fields. *PLoS One* **10**, e0117790 (2015).
53. Mahon, A. R., Mahon, H. K., Dauer, D. M. & Halanych, K. M. Discrete genetic boundaries of three *Streblospio* (Spionidae, Annelida) species and the status of *S. shrubsolii*. *Mar. Biol. Resear.* **5**, 172–178 (2009).
54. Meißner, K. & Blank, M. *Spiophanes norrisi* sp. nov. (Polychaeta: Spionidae) a new species from the NE Pacific coast, separated from the *Spiophanes bombyx* complex based on both morphological and genetic studies. *Zootaxa* **2278**, 1–25 (2009).
55. Funk, D. J. & Omland, K. E. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annu. Rev. Ecol. Evol. Syst.* **34**(1), 397–423 (2003).
56. Maciolek, N. J. A new genus and species of Spionidae (Annelida: Polychaeta) from the North and South Atlantic. *P. Biol. Soc. Wash.* **94**(1), 228–239 (1981).
57. Kongsrud, J. A. & Rapp, H. T. *Nicomache* (*Loxochona*) *lokii* sp. nov. (Annelida: Polychaeta: Maldanidae) from the Loki's Castle vent field: an important structure builder in an Arctic vent system. *Polar Biol.* **35**(2), 161–170 (2011).
58. Smirnov, R. V. Two new species of Pogonophora from the arctic mud volcano off northwestern Norway. *Sarsia* **85**, 141–150 (2000).
59. Eilertsen, M. H. *et al*. Genetic connectivity from the Arctic to the Antarctic: *Sclerolinum contortum* and *Nicomache lokii* (Annelida) are both widespread in reducing environments. *Sci. Rep.* **8**(1), 4810 (2018).
60. McClain, C. R. & Hardy, S. M. The dynamics of biogeographic ranges in the deep sea. *Proc. Royal Soc. B* **277**(1700), 3533–3546 (2010).
61. Linse, K. & Schwabe, E. Diversity of macrofaunal Mollusca of the abyssal Vema Fracture Zone and hadal Puerto Rico Trench, Tropical North Atlantic. *Deep-Sea Res. Pt II* **148**, 45–53 (2018).
62. Zardus, J. D., Etter, R. J., Chase, M. R., Rex, M. A. & Boyle, E. E. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). *Mol. Ecol.* **15**, 639–651 (2006).
63. Brix, S. *et al* Molecular species delimitation and its implications for species descriptions using desmosomatid and nannoniscid isopods from the VEMA fracture zone as example taxa. *Deep-Sea Res. Pt II* **148**, 180–207 (2018).
64. Scheltema, R. S. The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents in *Fourth European Marine Biology* Symposium (ed. Crisps, D. J.) 7–28 (London: Cambridge University Press 1971).
65. Geller, J., Meyer, C., Parker, M. & Hawk, H. Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Mol. Ecol. Resour.* **13**(5), 851–861 (2013).
66. Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotech.* **3**, 294–299 (1994).
67. Carpenter, J. M. & Wheeler, W. C. Towards simultaneous analysis of morphological and molecular data in Hymenoptera. *Zool. Scr.* **28**, 251–260 (1999).

68. Palumbi, S. R. Nucleic acids II: the polymerase chain reaction in *Molecular Systematics* Hillis, (eds Moritz, C., Mable, B. K.) 205–247 (Massachusetts: Sinauer & Associates Inc., Sunderland 1996).
69. Palumbi, S. R. *et al*. The Simple Fool's Guide to PCR, Version 2.0. Privately published, Univ. Hawaii (1991).
70. Dziķowski, R., Levy, M. G., Poore, M. F., Flowers, J. R. & Paperna, I. Use of rDNA polymorphism for identification of Heterophyidae infecting freshwater fishes. *Dis. Aquat. Organ.* **59**(1), 35–41 (2004).

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Author Contributions
First draft of the manuscript and figures were prepared by Theresa Guggolz. Martin Schwentner and Karin Meißner were proof-reading the manuscript, giving advices for interpreting the data and helping with analyses of data. Angelika Brandt was the head of the expedition and initiated the Vema-Transit project. She was also proof-reading the manuscript. The revision of the manuscript was mainly implemented by Theresa Guggolz with support of the co-authors.

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CHAPTER 5

High diversity and pan-oceanic distribution of deep-sea polychaetes: *Prionospio* and *Aurospio* (Annelida: Spionidae) in the Atlantic and Pacific Ocean

Manuscript submitted

High diversity and pan-oceanic distribution of deep-sea polychaetes: *Prionospio* and *Aurospio* (Annelida: Spionidae) in the Atlantic and Pacific Ocean

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Abstract

Prionospio Malmgren, 1967 and *Aurospio* Maciolek, 1981 (Annelida: Spionidae) are polychaete genera commonly found in the deep sea. Both genera belong to the *Prionospio* complex, whose members are known to have limited distinguishing characters. Morphological identification of specimens from the deep sea is challenging, as fragmentation and other damages are common during sampling. These issues impede investigations into the distribution patterns of these genera in the deep sea. In this study, we employ two molecular markers (16S and 18S) to study the diversity and the distribution patterns of *Prionospio* and *Aurospio* from the tropical North Atlantic, the Puerto Rico Trench and the central Pacific. Based on different molecular analyses (Automated Barcode Gap Discovery, pairwise genetic distances, phylogenetics, haplotype networks) we were able to identify and differentiate 21 lineages (three lineages composed solely of GenBank entries) that represent putative species. Seven of these lineages exhibited pan-oceanic distributions (occurring in the Atlantic as well as the Pacific) in some cases even sharing identical 16S haplotypes in both oceans. Even the lineages found to be restricted to one of the oceans were distributed over large regional scales as for example across the Mid-Atlantic Ridge from the Caribbean to the eastern Atlantic (> 3,389 km). Our results suggest that members of *Prionospio* and *Aurospio* have the potential to disperse across large geographic distances, largely unaffected by topographic barriers and even between oceans. Their high dispersal capacities are probably explained by their free-swimming long-lived planktonic larvae.

Keywords: distribution patterns, haplotype networks, Vema-Fracture-Zone, Clarion-Clipperton Fracture Zone, 16S, 18S

Introduction

The genus *Prionospio* Malmgren, 1867 is one of the most diverse and speciose taxa among Spionidae (Paterson et al. 2016; Guggolz et al. 2018). This genus is common and abundant in different shallow-water habitats but is most curiously also prevalent in the deep sea (Blake et al. 2017). *Prionospio* is morphologically not

well defined, even after several revisions and the erection of closely related subgenera and new genera in a *Prionospio* complex (Foster 1971; Maciolek 1985; Wilson 1990;Sigvaldadottir 1998). Currently the *Prionospio* complex comprises the genera (Sigvaldadottir 1998; Sigvaldadottir and Mackie 1993) *Aurospio* Maciolek, 1981a, *Laubieriellus* Maciolek, 1981b, *Orthoprionospio* Blake & Kudenov, 1978, *Prionospio* Malmgren, 1867, *Streblospio* Webster, 1879 and *Paraprionospio* Caullery (1914). Most of these revisions were mainly

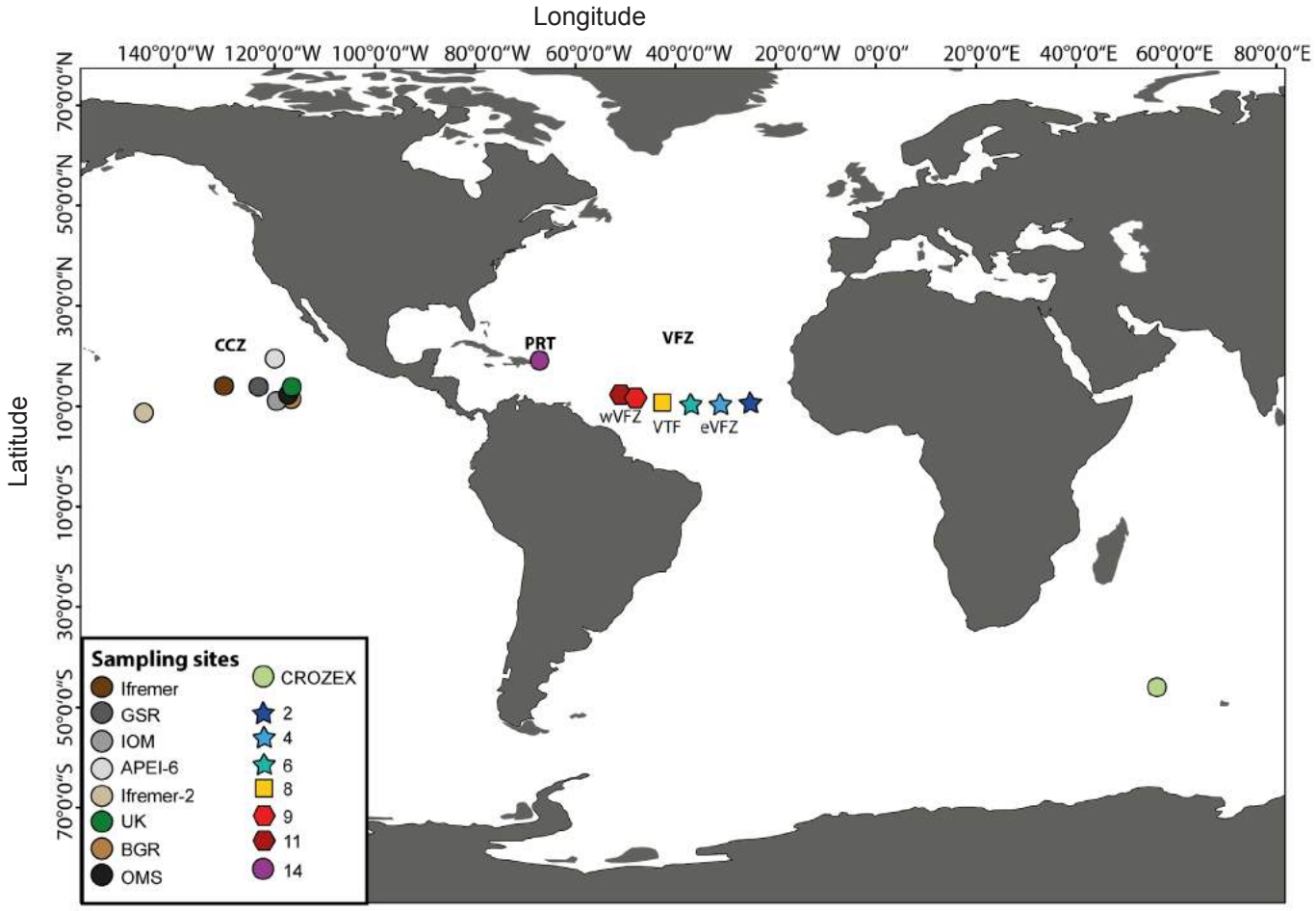

Figure 1. Map of the worldwide sampling localities. The Clarion Clipperton Fracture Zone (CCZ) in the Pacific, the eastern Vema Fracture zone (eVFZ – stars), the Vema Transform Fault (VTF – rectangular), the western Vema Fracture Zone (wVFZ – hexagon) and the Puerto Rico Trench (PRT).

based on shallow-water species, but *Prionospio* can also be regarded a typical deep-sea genus, often found in high abundances (Guggolz et al 2018; Blake and Maciolek 2017; Guggolz and Meißner pers. observations).

Despite the typical occurrence of *Prionospio* in deep-sea samples, the number of reported species is rather limited (Read and Fauchald 2018: 29 species - http://www.marinespecies.org/deepsea/). Only a few generic characters are available to distinguish between the genera of the *Prionospio* complex, often only the arrangement of the branchiae is important for the characterization of different subgenera and genera (Paterson et al 2016). These characters seem to be sufficient to identify specimens in appropriate conditions, but the morphological identification of these soft-bodied annelids from deep-sea samples is often difficult. Due to their fragility the majority of specimens from these depths are incomplete or damaged (Guggolz et al 2018; Guggolz et al. 2019; Bogantes et al. 2018). For example, the genus *Aurospio* is mainly distinguished from *Prionospio* by the number of the branchiae and on which segment they are beginning (Sigvaldadottir and Mackie 1993), but, these appendages are often lost or damaged during sampling procedures.

Species of both genera, *Prionospio* and *Aurospio*, are reported to be widespread (Paterson et al. 2016) or even cosmopolitan (Mincks et al. 2009) (e.g. *Aurospio dibranchiata* Maciolek, 1981a). A wide dispersal potential in the abyssal deep sea has been reported for many benthic invertebrates (Linse and Schwabe 2018; Schüller and Ebbe 2007; Etter et al. 2011); however, these distribution patterns based solely on morphological taxonomic identification have to be treated with caution. Recent studies, employing molecular tools, often indicated a more complex scenario. Several of these presumably widespread species were found to be composed of several geographically restricted and morphologically cryptic species (Vrijenhoek 2009; Bickford et al. 2007) or simply misidentified (Álvarez-Campos et al. 2017; Nygren et al. 2018;

Sun et al. 2016). Hence, hypothesizing distribution patterns in the deep sea is still challenging and integrative approaches, which combine morphological and molecular techniques, are essential to identify and delimit species (Hutchings and Kupriyanova 2018; Glover et al. 2016a). One important aspect of the present study is to examine the diversity and the dispersal capacity of *Prionospio* and *Aurospio* in the Vema-Fracture-Zone (VFZ). Both genera, *Prionospio* and *Aurospio,* are supposed to have planktonic larvae and thus a potential for a widespread geographic distribution (Young 2004; Wilson 1991). We investigate the dispersal along the VFZ and test for barrier effect of the Mid-Atlantic Ridge (MAR) as this underwater mountain ridge is often postulated to represent a topographic barrier for distribution of benthic invertebrates (Bober et al. 2018; McClain et al. 2009; Priede et al. 2013). However, a barrier effect of the MAR on the spionid *Laonice* Malmgren, 1867 has recently been rejected (Guggolz et al. 2019). The herein studied *Prionospio* and *Aurospio* will be another important step towards understanding the distribution patterns of species in the deep sea along the MAR. In addition, a potential pan-oceanic distribution is analyzed, by comparing DNA sequences of specimens from the VFZ (tropical Atlantic) with those of the Clarion-Clipperton Fracture Zone (CCZ) from the central Pacific.

Material and Methods

Collection and identification of specimens

During the VEMA-Transit expedition in December 2014–January 2015 197 of the 332 analysed specimens were collected from the tropical North Atlantic and the Puerto Rico Trench (Fig. 1: VFZ and PRT). Detailed information about sample treatment and sampling localities are described in Guggolz et al. (2018) and Devey et al. (2015). Four areas were defined for samples from the Atlantic according to the geographical position as following: the eastern part of the Vema-Fracture Zone (eVFZ), extending eastwards from the MAR in the Cape Verde Basin; the western part of the Vema Fracture Zone (wVFZ), extending westwards from the MAR in the Demerara Basin; the Vema Transform Fault (VTF), located between these two areas in the MAR; the Puerto Rico Trench (PRT), located in the shallower part of the trench near Puerto Rico. Maximum distances within areas varied between 276 km (wVFZ) and 1,298 km (eVFZ). The eastern-most and western-most studied sites were separated by 4,610 km.

The Clarion-Clipperton Fracture Zone (CCZ) is a vast area (about 6 million km^2) in the Equatorial Pacific Ocean with high commercial interest because of the presence of polymetallic nodules in the seabed between 4000 and 5000 m depth. The International Seabed Authority (ISA) is in charge of management of deep-sea mineral resources and of protection of marine environment in areas beyond national jurisdiction (Lodge et al. 2014). The ISA provides licenses to the contractors, that intend to explore mineral deposits in e.g. the CCZ. To get and keep an exploration contract for an area, the contractor is required to carry out surveys and fauna inventories (Lodge et al. 2014). Furthermore, the ISA administrates the regional environmental management plan across the CCZ, so-called Areas of Particular Environmental Interest (APEI). Sequences of 122 specimens from eight exploration contract areas and one APEI were included (Fig. 1: the German exploration contract area 'BGR', Russia and Poland among other countries 'IOM', Belgium 'GSR', French 'Ifremer' & 'Ifremer-2', Singapore 'OMS', Britain UK-1 and the APEI-6). Of these, 53 specimens were collected on the two United Kingdom Seabed Resources Ltd (UKSR) cruises AB01 and AB02 to the UK-1 exploration contract area stratum A and stratum B, the OMS contract area, and the APEI-6. Details on sampling methods are given in Glover et al. (2016a)[28]. Maps and metadata from UK-1 stratum A has been published in earlier taxonomical work on macrofaunal material from these cruise (Glover et al. 2016a; Dahlgren et al. 2016; Wiklund et al. 2017; Wiklund et al. submitted). In addition, 69 specimens from BGR, IOM, GSR and Ifremer were sampled using box-corers (0.25 m^2) or epibenthic sledge during EcoResponse SO239 cruise on board of the RV *Sonne* in March/April 2015 funded by JPI Oceans framework (Martínez-Arbizu and Haeckel 2015).

All specimens were sorted and identified at least to genus level (*Prionospio* or *Aurospio*) using dissecting and compound microscopes. Specimens have been deposited in the collection of the Center of Natural History (Universität Hamburg, Germany), Ifremer (France) and Natural History Museum London (Supplement 1).

The map of the sampling areas (Fig. 1) was created using ArcGIS 10.4.1 (www.esri.com).

DNA extraction, PCR amplification, sequencing and alignment

For the VFZ specimens, one or two parapodia were dissected and transferred into 30 µl of 10 % Chelex 100 solution in purified water, incubated for 30 minutes at 56°C and 10 minutes at 99°C. Polymerase Chain Reactions (PCR) were performed with a total volume of 15 µl consisting of 1.5 µl DNA extract, 7.5 µl AccuStart II PCR ToughMix (Quanta Bio, Germany), 0.6 µl of each primer (10mmol), 0.3 µl of GelTrack loading dye (QuantaBio, Germany) and 4.8 µl Millipore H_2O. Fragments of mitochondrial (16S) and nuclear (18S) rRNA genes were amplified (see Table 1 for list of primers) with initial denaturation step of 94°C for 3 min, followed by 35 cycles of 30 s at 94°C, 45 s at 43°C and 45 sec at 72°C, followed by a final elongation step for 5 min at 72°C. Success of amplification was determined via gel electrophoresis on 1 % agarose/ TAE gel. For sequencing, 8 µl of the PCR products were purified using FastAP (1.6 µl; 1U/µl) and Exonuclease I (0.8 µl;20U/µl) (Thermo Fisher Scientific, Germany) with an incubation time of 37°C for 15 min followed by 15 min at 85°C. For a some of the specimens from the CCZ (BGR, IOM, GSR and Ifremer), DNA extractions were realised with NucleoSpin Tissue (Macherey-Nagel) kit and PCR amplifications as following into 25 µL mixtures, including: 5 µL of Green GoTaq® Flexi Buffer (final concentration of 1X), 2.5 µL of MgCl2 solution (final concentration of 2.5 mM), 0.5 µL of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 9.875 µL of nuclease-free water, 2.5 µL of each primer (final concentration of 1 µM), 2 µL template DNA and 0.125 U of GoTaq® G2 Flexi DNA Polymerase (Promega). The temperature profile was: 95°C/240s — (94°C/30s-52°C/60s-72°C/75s *35 cycles) — 72°C/480s — 4°C. Purified PCR products were sent to Macrogen Europe, Inc. (Amsterdam-Zuidoost, Netherlands) for sequencing. The remaining specimens from the CCZ (APEI-6, OMS, UK-1) were extracted with DNeasy Blood and Tissue Kit (Qiagen) using a Hamilton Microlab STAR Robotic Workstation. PCR mixtures contained 1 µl of each primer (10µM), 2 µl template DNA and 21 µl of Red Taq DNA Polymerase 1.1X MasterMix (VWR) in a mixture of total 25 µl. The PCR amplification profile consisted of initial denaturation at 95°C for 5 min, 35 cycles of denaturation at 94°C for 45 s, annealing at 55°C for 45 s, extension at 72°C for 2 min, and a final extension at 72°C for 10 min. PCR products were purified using Millipore Multiscreen 96-well PCR Purification System, and sequencing was performed on an ABI 3730XL DNA Analyser (Applied Biosystems) at Natural History

Table 1. Primers used in this study.

Gene	Primer	Primer sequence 5'-3'	Authors
16S	16Sar	CGCCTGTTTATCAAAAACAT	Palumbi, 1996
	16Sbr	CCGGTCTGAACTCAGATCACGT	Palumbi, 1996
	16Sb-L	CCGGTCTGAACTCAGATCACGT	Palumbi et al., 1991
	Ann16SF	GCGGTATCCTGACCGTRCWAAGGTA	Sjölin et al. 2005
18S	Uni 18S F	GCTTGTCTCAGAGATTAAGCC	Dzikowski et al., 2004
	HET 18S R	ACGGAAACCTTGTTACGA	Dzikowski et al., 2004
	18SA	AYCTGGTTGATCCTGCCAGT	Medlin et al. 1988
	18SB	ACCTTGTTACGACTTTTACTTCCTC	Nygren and Sundberg 2003
	620F	TAAAGYTGYTGCAGTTAAA	Nygren and Sundberg 2003
	1324R	CGGCCATGCACCACC	Cohen et al. 1998

Museum Sequencing Facility, using the same primers as in the PCR reactions.

In total, 331 specimens were successfully sequenced for 16S and 63 specimens for 18S. Sequences were assembled and corrected with Geneious 6.1.8 (Kearse et al. 2015; http://www.geneious.com) and deposited in GenBank (for accession numbers see Supplement Table 1). The obtained sequences of the different gene fragments were aligned separately using MAFFT (Katoh and Standley 2013; V 7.402) implemented with CIPRES Science Gateway V.3.3 (Miller et al. 2010; www.phylo.org).

Initial identification of species, phylogenetic analyses and haplotype networks

To obtain a first estimation of the number of species present in our data set, the Automated Barcode Gap Discovery (Puillandre et al. 2012; ABGD) was conducted with 16S. The ABGD identifies potential barcoding gaps separating hypothetical species, which is based on the assumption that interspecific genetic distances are larger than intraspecific distances. The ABGD analysis was run on the web-based version of the software (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html). Pairwise uncorrected *p*-distances were used for the analyses (Table 2), which were calculated with MEGA7 (Kumar et al. 2016), including all available sequences for each gene, respectively. Standard settings for ABGD were kept, except for Pmin (0.005), the numbers of steps (100) and the relative gap width (X=0.5). In the following we will use the term lineages rather than species for the units delimited by ABGD, as not all of these might correspond to actual species.

To assess the phylogenetic relationships among the studied specimens and to assess whether the lineages suggested by ABGD are monophyletic, phylogenetic analyses were performed with Bayesian inference and maximum likelihood. Both gene fragments were analysed separately, as well as concatenated with MrBayes (Ronquist and Huelsenbeck 2003; version 3.2). The maximum likelihood was performed using Randomized Axelerated Maximum Likelihood (Stamatakis 2014; RAxML v.8.2.10) on XSEDE with rapid bootstrapping (1000 iterations) via the CIPRES Science Gateway V.3.3 (Miller et al. 2010; www.phylo.org). Due to missing sequences of the 18S genes for a large part of the analysed specimens and the very few mutations, only the phylogenetic analysis of the 16S gene is included. For the 16S analysis different spionids that are not assigned to the *Prionospio* complex were chosen as outgroups (Supplement 1). Additionally, available 16S sequences of *Prionospio* and *Aurospio* from GenBank were included in the analyses (Supplement 1). Four chains were run for $5*10^7$ generations, with sampling every 1200^{th} generation, and discarding the first 25 % as burn-in. Thus, the convergence chain runs were validated using TRACER v.1.7.1 (Rambaut et al. 2018). The GTR + I + G substitution model was identified by MEGA7 as the best fitting model under the AIC criterion.

To better visualize the geographic distribution of the genetic diversity median-joining haplotype networks were generated with Network 5.0.0.3 (http://fluxus-engineering.com/) and popART 1.7 (Bandelt et al. 1999) for each gene fragment. In 16S, networks were calculated separately for each lineage. The generated haplotype networks were redrawn with Adobe Illustrator CS6.

Analyses of population differentiation were performed with Arlequin 3.5 (Excoffier and Lischer 2010) for lineages with sufficiently large specimen numbers (at least four specimens per site). Pairwise Φst was calculated different lineages identified as *Aurospio* cf. *dibranchiata*, *Aurospio* sp. S and *Prionospio* sp. B, sp.H (16S). For *Aurospio* cf. *dibranchiata* areas eVFZ, wVFZ and CCZ, for *Aurospio* sp. S areas eVFZ and CCZ and for *Prionospio* sp. B the areas eVFZ, VTF and CCZ and for *Prionospio* sp. G the sites 2 and 4 were compared (Table 3, 4).

Results

Alignment

The alignment of the 16S fragment included a total of 331 sequences with a minimum length of 442

Table 2. Percentage of uncorrected p-distances within (diagonal panels) and among lineages (upper panels) for 16S (bold) and 18S (regular). “X” means no or only one sequence available.

	P. sp. A	*P.*sp. B	*P.* sp. C	*P.* sp. D	*A.* cf. *di-branchiata*	*P.* sp. E	*P.* sp. F	*A. food-bancsia*	*P.* sp. G	*P.* sp. H	*P.* sp. I	*P.* sp. K	*P.* sp. L	*P.* sp. M	*P.* sp. N	*P.* sp. O	*P.* sp. P	*P.* sp. Q	*A.* sp. R	A. sp. S	*A.* sp. T
Prionospio sp. A	**0.7 - 2.0** X	**20.2 - 22.2** X	**21.6 - 22.4** X	**20.6 - 22.7** X	**23.1 - 27.6** X	**21.0-24.8** X	**20.4 - 21.6** X	**24.6 - 25.8** X	**20.5 - 21.0** X	**22.8 - 28.7** X	**20.0 - 20.5** X	**23.8 - 25.0** X	**24.0 - 26.6** X	**25.0 - 25.7** X	**24.0 - 26.8** X	**25.2 - 26.4** X	**23.0 - 25.5** X	**28.8 - 29.0** X	**23.3 - 23.0** X	**20.9 - 22.8** X	**24.0 - 26.7** X
Prionospio sp. B		**0 -1.2** 0	**8.4 - 10.3** 0	**9.5 -15.9** 0	**18.6 - 22.1** 0.3	**17.6 -22.5** X	**13.6 - 15.3** X	**18.6 - 21.9** 0.7	**10.0 - 16.0** 0.1	**18.8 - 24.1** 0.8 – 0.9	**17.0 - 18.7** 0.8	**19.8 - 21.7** X	**18.9 - 22.2** 0.7	**21.4 - 25.5** 0.7	**18.2 - 22.6** 0.7	**20.0 - 22.4** 0.9	**20.1 - 22.2** 0.5	**22.6 - 23.7** X	**20.5 - 21.7** X	**17.8 - 21.5** 0.3	**18.2 - 21.8** X
Prionospio sp. C			**0 - 0.2** 0	**5.1 - 6.2** 0	**18.3 - 22.5** 0.3	**18.6 - 22.4** X	**14.6 - 15.1** X	**19.3 - 20.5** 0.7	**13.7 - 14.4** 0.1	**18.7 - 22.9** 0.8 – 0.9	**18.5 - 18.6** 0.8	**18.3 - 18.8** X	**14.2 - 21.6** 0.7	**22.1 - 23.1** 0.7	**18.2 - 23.2** 0.7	**19.7 - 22.8** 0.9	**20.4 - 22.4** 0.5	**22.9 - 23.3** X	**20.5** X	**18.8 - 21.5** 0.3	**18.2 - 22.4** X
Prionospio sp. D				**0 – 0.5** X	**16.8 - 23.9** 0.3	**15.9 - 22.7** X	**14.8 - 16.1** X	**19.6 - 21.3** 0.7	**15.4- 16.5** 0.1	**18.0 - 24.3** 0.8 – 0.9	**18.3 - 21.0** 0.8	**19.5 - 21.0** X	**15.8 - 22.4** 0.7	**18.9 - 24.3** 0.7	**16.5 - 24.4** 0.7	**21.0 - 24.1** 0.9	**19.7 - 23.2** 0.4	**21.9 - 23.9** X	**21.2 - 23.0** X	**15.6 - 22.0** 0.3	**15.9 - 23.5** X
Aurospio cf. *dibranchiata*					**0 - 2.9** 0	**20.4 - 26.5** X	**16.2 - 18.7** X	**22.2 - 28.1** 0.5	**16.7 - 21.1** 0.4	**19.6 - 21.7** 0.7 – 0.8	**18.9 - 21.7** 0.7	**22.8 - 27.4** X	**22.9 - 27.8** 0.5	**22.4 - 28.2** 0.5	**12.8 - 27.8** 0.5	**22.7 - 27.2** 0.5	**19.0 27.0** 1.1	**25.9 - 28.2** X	**24.0 - 27.5** X	**13.2 - 16.9** 0	**12.3 - 27.1** X
Prionospio sp. E						**0 - 3.3** X	**18.6 - 20.9** X	**21.5 - 25.7** 1.3	**15.6 - 21.2** 1.9	**21.6 - 32.2** 1.4 – 1.5	**18.4 - 22.0** 1.4	**23.9 - 27.8** X	**22.7 - 29.1** 1.3	**23.4 -28.7** 1.3	**21.4 - 28.4** 1.3	**25.0 - 28.0** 1.5	**20.7 - 24.1** X	**25.1 - 27.9** X	**25.6 - 28.8** X	**19.8 - 24.1** 1.6	**21.4 - 27.4** X
Prionospio sp. F							**X** X	**20.5 - 21.2** X	**14.5 - 14.8** X	**17.4 - 21.3** X	**17.5** X	**20.6** X	**19.4 - 20.7** X	**21.3 - 22.3** X	**17.6 - 22.3** X	**22.5 - 22.8** X	**18.7 - 20.1** 0.1	**22.3** X	**22.6** X	**17.7 - 17.9** X	**17.3 - 21.3** X
Aurospio foodbancsia								**0 - 1.2** X	**19.7 - 20.7** 0.8	**21.5 - 27.3** 0.5 -0.7	**20.3 - 20.7** 0.5	**16.3 - 17.0** X	**12.8 - 13.8** 0	**15.1 - 16.3** 0	**18.2 - 21.5** 0	**18.5 - 20.0** 0.2	**21.0 - 22.5** 0.7	**24.7 - 25.7** X	**19.5 - 20.0** X	**21.3 - 24.1** 0.5	**18.1 - 23.4** X

Table 2 (continued)

	P. sp. A	*P.*sp. B	*P.* sp. C	*P.* sp. D	*A.* cf. *di-branchiata*	*P.* sp. E	*P.* sp. F	*A. food-bancsia*	*P.* sp. G	*P.* sp. H	*P.* sp. I	*P.* sp. K	*P.* sp. L	*P.* sp. M	*P.* sp. N	*P.* sp. O	*P.* sp. P	*P.* sp. Q	*A.* sp. R	A. sp. S	*A.* sp. T
Prionospio sp. G									**0 - 2.5** 0	**18.3 - 24.3** 0.9 - 1.0	**16.4 - 16.7** 0.9	**20.4 - 20.7** X	**18.4 - 20.3** 0.8	**18.9 - 20.2** 0.8	**15.9 - 24.4** 0.8	**23.7 - 24.4** 0.1	**21.8 - 23.5** 0.2 – 0.3	**23.7 - 23.9** X	**22.2- 22.5** X	**15.3 - 17.1** 0.4	**15.6 - 23.5** X
Prionospio sp. H										**0 - 4.8** 0 – 0.1	**11.6 - 16.6** 0	**20.1 - 25.9** X	**20.9 - 26.9** 0.3 – 0.4	**22.7 - 30.1** 0.3 – 0.4	**17.8 - 27.1** 0.3 – 0.4	**23.9 - 27.2** 0.5 – 0.7	**21.3 - 28.5** 0.2	**26.6 - 32.0** X	**24.5 - 28.8** X	**20.1 - 26.2** 0.7 – 0.8	**18.0 - 26.7** X
Prionospio sp. I											**X** X	**21.2** X	**22.0 - 23.0** 0.3	**23.4 - 24.2** 0.3	**18.4 - 23.7** 0.3	**24.2 - 24.4** 0.5	**21.6 - 22.9** X	**24.9** X	**23.6** X	**19.4 - 21.9** 0.7	**18.2 - 23.4** X
Prionospio sp. K												**X** X	**13.9 - 14.0** X	**17.8 - 18.0** X	**14.7 - 21.0** X	**15.5 - 15.6** X	**22.7 - 23.7** 0.2	**25.6** X	**16.4** X	**22.7 - 24.7** X	**23.1** X
Prionospio sp. L													**0 - 4.9** 0	**15.2 - 16.9** 0	**16.8 - 21.4** 0	**17.8 - 19.3** 0.2	**23.6 - 25.8** 0.2	**25.2 - 25.5** X	**18.4 - 19.5** X	**21.5 - 25.3** 0.5	**16.2 - 24.2** X
Prionospio sp. M														**0 - 1.7** 0	**21.5 - 22.9** 0	**21.8 - 22.1** 0.2	**23.2 - 24.2** 0.2	**28.6 - 29.2** X	**19.4 - 19.7** X	**22.0 - 25.3** 0.5	**21.5 - 25.5** X
Prionospio sp. N															**0 - 5.8** X	**5.2 - 5.9** 0.2	**21.1 - 22.6** 0.2	**24.8 - 25.3** X	**14.9** X	**23.1 - 23.7** 0.5	**23.1 - 25.9** X
Prionospio sp. O																**0 - 0.8** X	**21.0 - 22.0** 0.3	**25.3 - 25.5** X	**14.4 - 14.7** x	**22.7 - 23.7** 0.8	**22.4 - 25.5** X

Table 2 (continued)

	P. sp. A	*P.*sp. B	*P.* sp. C	*P.* sp. D	*A.* cf. *dibranchiata*	*P.* sp. E	*P.* sp. F	*A. foodbancsia*	*P.* sp. G	*P.* sp. H	*P.* sp. I	*P.* sp. K	*P.* sp. L	*P.* sp. M	*P.* sp. N	*P.* sp. O	*P.* sp. P	*P.* sp. Q	*A.* sp. R	*A.* sp. S	*A.* sp. T
Prionospio sp. P																	**0 - 0.8**	**24.0 - 26.0**	**24.0 - 24.7**	**21.5 - 23.7**	**21.8 - 26.2**
																	X	X	X	0.4	X
Prionospio sp. Q																		**X**	**24.7**	**27.4 - 28.1**	**26.5 - 29.0**
																		X	X	X	X
Aurospio sp. R																			**X**	24.9	**24.9 - 28.0**
																			X	X	X
Aurospio sp. S																				**0 – 0.7**	**8.0 - 10.3**
																				0	X
Aurospio sp. T	16S																				**0 - 1.4**
	18S																				X

base pairs (bp), of which 237 bp were variable and 223 bp were parsimony informative. The alignment of the 18S fragment consisted of 59 sequences with 845 bp minimum, of which 25 bp were variable and 20 bp were parsimony informative.

Species delimitation and diversity

The ABGD analysis of the 16S dataset retrieved 21 main lineages when a barcode gap threshold of 1

4.9 % was employed. The 21 lineages were designated to *Prionospio* sp. A to sp. P, *Aurospio* sp. Q to sp. T, as well as *Aurospio* cf. *dibranchiata* and *Aurospio foodbancsia* Mincks, Dyal, Paterson, Smith & Glover, 2009. The lineage *Aurospio* cf. *dibranchiata* is named according to corresponding GenBank records assigned in the analyses (Supplement 1), but with reservation, as no genetic data is available for the holotype or from the type locality. With higher barcode threshold values several lineages collapsed (5.1 5.2 % = 20 lineages: lineages C and D collapse; 5.4 8.5 % = 19 lineages: lineages N and O collapse).

Pairwise genetic distances (uncorrected *p*-distances) between the 21 lineages varied for 16S from 5.1 32.0 % (based on the 21 lineages derived from 16S) (Table 2). The lowest pairwise distances were found between lineages C and D (16S: 5.1 6.2 %), as well as between lineages N and O (16S: 5.2 – 5.9 %; Table 2). All other inter-lineage distances exceeded 8.5 % for 16S. The highest observed intra-lineage distances were found in lineage H with 4.8 % for 16S (Table 2). Pairwise distances between the single lineages found for 18S varied from 0 – 1.9 %, with highest distances between lineage *Prionospio* sp. E and sp. G and the highest intra-lineage pairwise distances were found for lineage E with 0.1 % (Table 2).

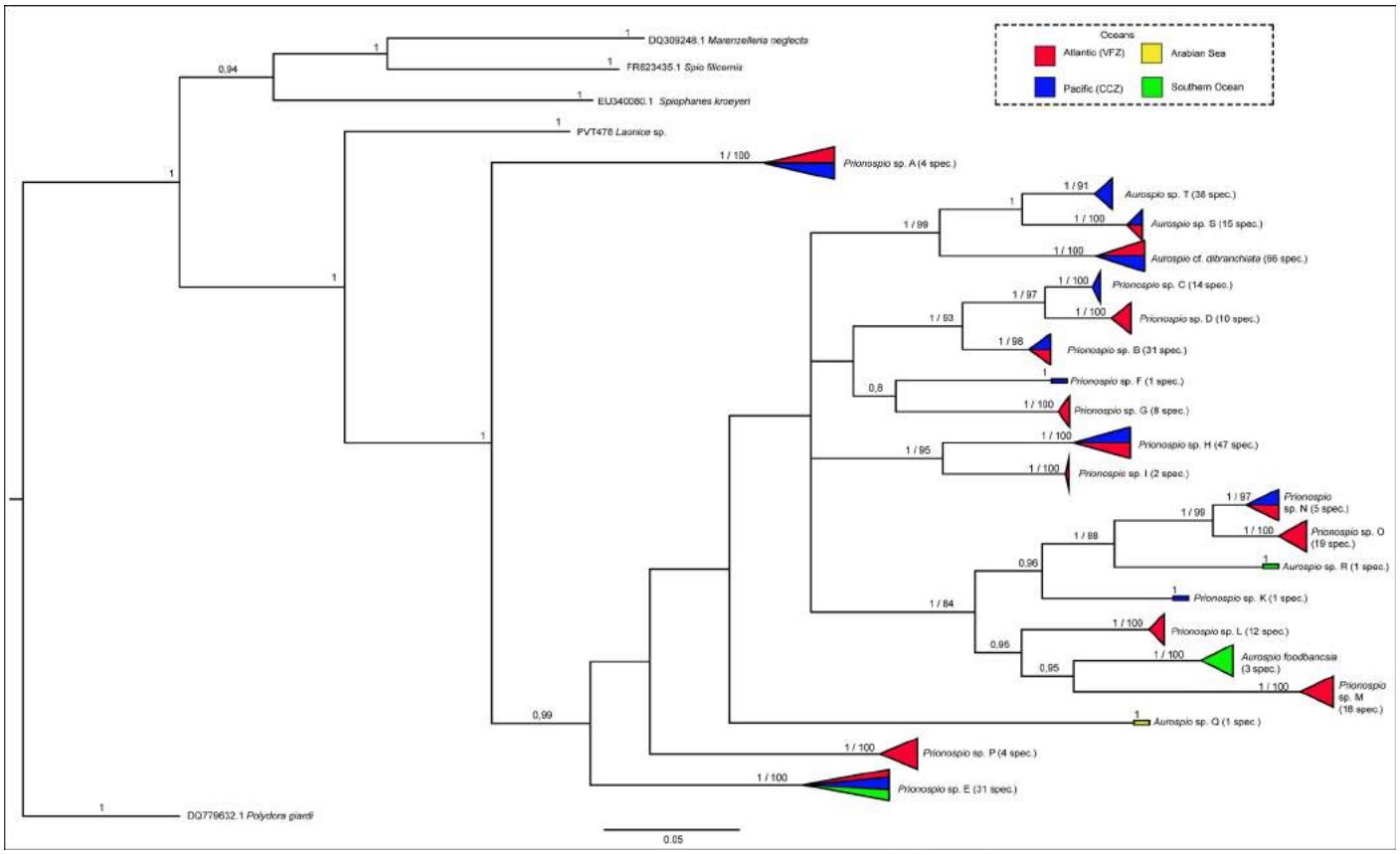

Figure 2. Phylogenetic tree of Prionospio *and* Aurospio *species obtained in the study based on mitochondrial 16S gene fragments. Individual specimens can be found in Supplement 2. Posterior probabilities shown next to the nodes (values below 0.8 are not shown); Bootstrap values are shown after slashes (values below 80 are not shown). Numbers of specimens are given in brackets. Individual occurrence in different oceans is colour coded non proportional (see legend in the right upper corner).*

The phylogenetic analyses of 16S recovered all 21 lineages as reciprocal monophyletic with full support each (Fig. 2; supplement 2). The two genera were not recovered as monophyletic as *Aurospio foodbancsia*, *Aurospio* sp. R and *Aurospio* sp. Q were nested among the *Prionospio* lineages (Fig. 2) and *Aurospio* sp. S, sp. T and *Aurospio* cf. *dibranchiata* formed a monophyletic clade but also this clade was nested within *Prionospio* lineages (Fig. 2).

In the haplotype networks of 16S (Fig. 3) a total of 128 haplotypes (h1-16S h128-16S) were found with a maximum of 28 haplotypes in one lineage (*Prionospio* sp. H, h31-16S h58-16S; Fig. 3). Notably, *Prionospio* H and *Aurospio* cf. *dibranchiata* had the highest intra-lineage 16S distances with up to 4.8 % and in both cases these high distances were observed among individuals from Atlantic and Pacific oceans. However, other individuals from these regions either shared 16S haplotypes or featured haplotypes separated by only 1.3 % (Fig. 3, Table 2).

The 18S network showed a total of 18 genotypes (h1-18S h18-18S, Fig. 4). The lineages *Prionospio* sp. D, sp. E, sp. G, sp. O and sp. P are well differentiated from each other, while other lineages shared genotypes and cluster together with no or one mutational step (*Prionospio* sp. L, sp. M, sp. N and *Aurospio foodbancsia*; *Prionospio* sp. H and sp. I; *Prionospio* sp. B and sp. C; *Aurospio* cf. *dibranchiata* and *Aurospio* sp. S; Fig. 4).

For several *Prionospio* and *Aurospio* lineages pan-oceanic distributions with occurrences in the Atlantic as well as Pacific were recorded. *Prionospio* sp. A, sp. B, sp. E, sp. H, sp. L, and sp. N, as well as *Aurospio* sp. S and *Aurospio* cf. *dibranchiata* were recorded from the VFZ in the Atlantic and the CCZ in the Pacific whereas *Aurospio* cf. *dibranchiata* and *Prionospio* sp. E occurred furthermore in the Southern Ocean (Fig. 2, Supplement 2). However, not only lineages, but also several 16S haplotypes were shared between specimens from the Pacific and the Atlantic (*Prionospio* sp. B, h9-16S; *Prionospio* sp. H, h35-16S; *Prionspio* sp. L, h62-16S; *Aurospio* sp. S, h87-16S; *Aurospio* cf. *dibranchiata*, h111-16S; Fig.

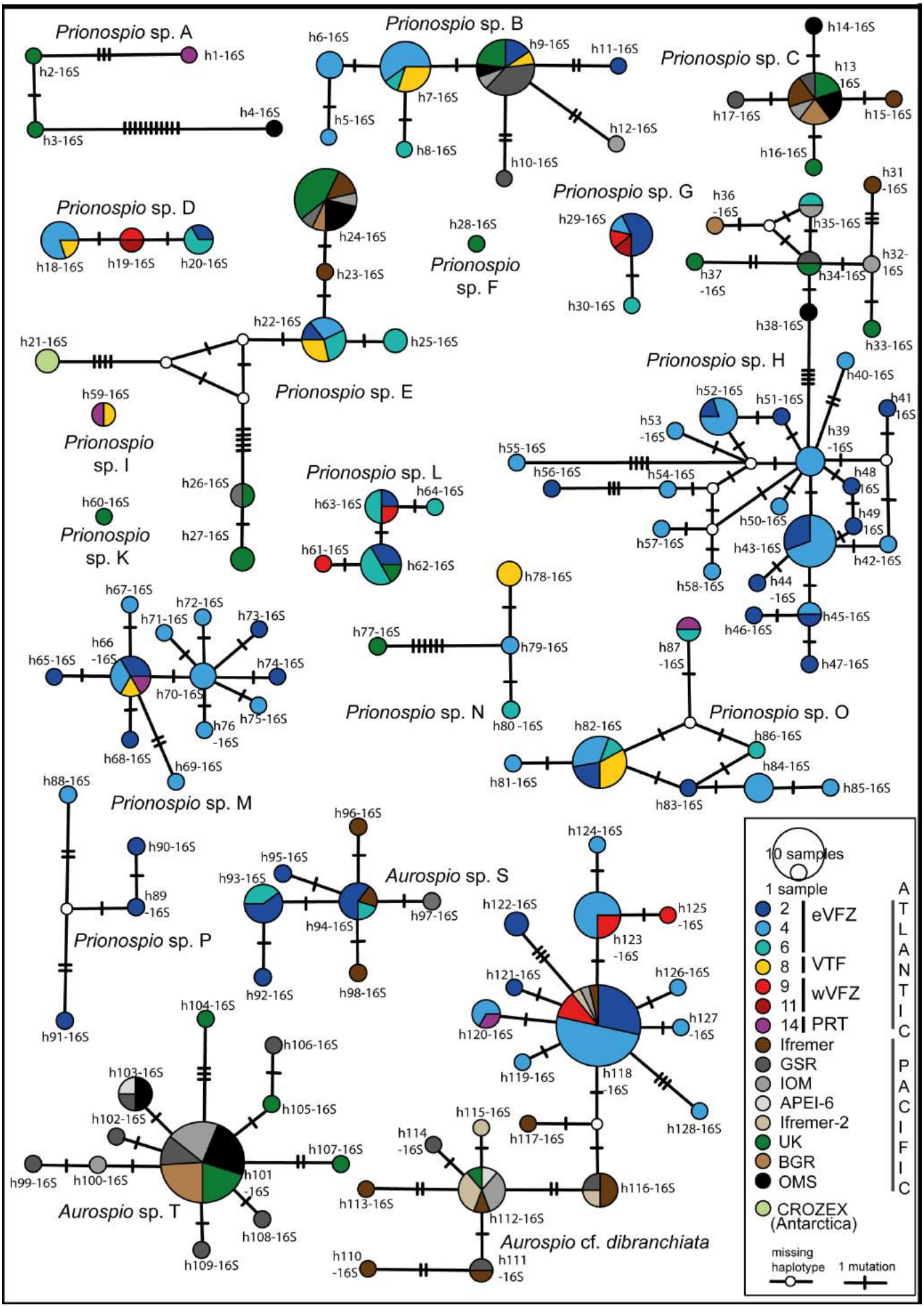

Figure 3. Haplotype networks of Prionospio *and* Aurospio *species from the different localities of 16S gene fragments. Sampling localities are colour coded.*

Table 3. Population indices for 16S of selected *Prionospio* or *Aurospio* species among geographic areas and oceans. Nucleotide diversity, Tajima's D and Fu's Fs are reported only for the areas, not the individual areas. (eVFZ: eastern Vema Fracture Zone, wVFZ: western Vema-Fracture Zone, VTF: Vema Transform Fault, CCZ: Clarion-Clipperton Fracture Zone)

	area	No. of ind.	No. of haplotypes	Nucleotide diversity ± SD		Tajima's D (p-value)	Fu's F_s (p-value)
***Prionospio* sp. B**							
Atlantic	eVFZ	15	8	0.0039 +/-	0.002	-0.897 (0.18)	-1.999 (0.06)
	VTF	4	2	0.0015 +/-	0.0019		
Pacific	CCZ	12	4	0.0056 +/-	0.0039	0.000 (1.00)	2.076 (0.86)
***Prionospio* sp. H**							
Atlantic	eVFZ	38	22	0.0101 +/-	0.0060	-1.730 (0.03)	-14.396 (0.00)
Pacific	CCZ	9	8	0.0091 +/-	0.0062	-1.166 (0.13)	-5.062 (0.00)
***Aurospio* sp. S**							
Atlantic	eVFZ	11	4	0.0026 +/-	0.0022	-0.384 (0.32)	-0.939 (0.12)
Pacific	CCZ	4	3	0.0029 +/-	0.0029	-0.709 (0.28)	-0.887 (0.10)
Aurospio* cf. *dibranchiata							
Atlantic	eVFZ	36	12	0.0052 +/-	0.0034	-1.471 (0.05)	-5.703 (0.00)
	wVFZ	7	5	0.0053 +/-	0.0039		
Pacific	CCZ	24	8	0.0074 +/-	0.0046	0.112 (0.59)	-0.208 (0.50)

3).

Thirteen of the identified lineages were restricted to one of the sampled oceans: *Prionospio* sp. D, sp. G, sp. I, sp. M, sp. O and sp. P to the Atlantic; *Prionospio* sp. C, sp. F, sp. K and *Aurospio* sp. T to the Pacific; *Aurospio foodbancsia* and *Aurospio* sp. R to the Southern Ocean; and *Aurospio* sp. Q to the Arabian Sea (Fig. 2). Moreover, some of these lineages were distributed over larger regional scales within these oceans and sea. For instance, *Prionospio* sp. G had one haplotype recorded from the eVFZ and the wVFZ (Fig. 3: h29-16S) and *Prionospio* sp. L even shared a haplotype between the eVFZ and the PRT (Fig. 3: h61-16S).

Population differentiation was significant between the Atlantic and Pacific specimens for lineage *Prionospio* sp. H, *Aurospio* cf. *dibranchiata* and *A*urospio sp. S (Table 4). For *Aurospio* cf. *dibranchiata* significant differences were also found within the Atlantic population (eVFZ and VTF; Table 4). The lineage *Prionospio* sp. B showed significant difference between the population from the eVFZ and the population from the Pacific, but no significant differences between the specimens from the VTF and the Pacific were found (Table 4). Tajima's D and Fu's F_s reveal significant negative values for *Prionospio* sp. H (Table 4). *Aurospio* cf. *dibranchiata* showed also negative significant values, but only for the Atlantic population (Table 3: Fu's F_s).

Discussion

In the present study based on the mitochondrial marker 16S gene, 21 lineages were identified consistently and well supported for *Prionospio* and *Aurospio* from the deep Atlantic and Pacific. But limits of mitochondrial markers for species delimitation

are well known, as mitochondrial DNA poses potential risks like the retention of ancestral polymorphism, male-biased gene flow, hybrid introgression and paralogy (Moritz and Cicero 2004; Galtier et al. 2009).

***Prionospio* sp. B**	**Atlantic**		**Pacific**
	eVFZ	VTF	CCZ
eVFZ	0.00		
VTF	0.00	0.00	
CCZ	0.31*	0.20	0.00

***Prionospio* sp. H**	**Atlantic**	**Pacific**
	eVFZ	CCZ
eVFZ	0.00	
CCZ	0.31*	0.00

***Aurospio* sp. S**	**Atlantic**	**Pacific**
	eVFZ	CCZ
eVFZ	0.00	
CCZ	0.23*	0.00

Aurospio* cf. *dibranchiata	**Atlantic**		**Pacific**
	eVFZ	VTF	CCZ
eVFZ	0.00		
wVFZ	0.15*	0.00	
CCZ	0.58*	0.54*	0.00

Table 4. Pairwise Φst values among different sites for 16S of selected *Prionospio* or *Aurospio* species among areas. Asterisk indicating significant p-values.

(eVFZ: eastern Vema Fracture Zone, wVFZ: western Vema-Fracture Zone, VTF: Vema Transform Fault; CCZ: Clarion-Cipperton Fracture Zone)

All lineages, which share an identical 18S genotype, had uncorrected pairwise distances exceeding 8.4 % in 16S (lineages B and C: 8.4 10.3 %; lineages H and I: 11.6–16.6 %; lineages L, M, N and *Aurospio foodbancsia*: 12.8 22.9 %; lineages *Aurospio* cf. *dibranchiata* and S: 13.2 16.9 %) and the intraspecific uncorrected distances were always lower within these lineages (16S: 0 – 5.8 %). The levels of interspecific differentiation in 16S are comparable to those observed among other polychaete species, which usually exceeded 5 % for the mitochondrial marker 16S gene (Álvarez-Campos et al. 2017; Meißner et al. 2016; Brasier et al. 2016; Wiklund et al. 2009). We imply thresholds about 5 – 6 % for 16S to distinguish between *Prionospio* and *Aurospio* species. In a recent study, Guggolz et al. (2019) found barcoding gaps of ~2 – 2.8 % in 16S between *Laonice* species, another spionid genus, from the tropical Atlantic. The fact that we found higher intraspecific distances, in particular within *Prionospio* sp. H and *Aurospio* cf. *dibranchiata*, might be explained by the larger geographic sampling in our study. It appears likely that the overall intraspecific diversity would be higher if additional regions and populations were studied. Based on the available data we postulate that each one of the 21 lineages represents a separate species within the investigated dataset. Of these *Aurospio foodbancsia*, *Aurospio*, sp. Q and sp. R were studied solely on the basis of sequence data obtained from GenBank. One has to keep in mind that a higher number of species might be present within the dataset (e.g. *Prionospio* sp. E and sp. A might be further split) using a less con-

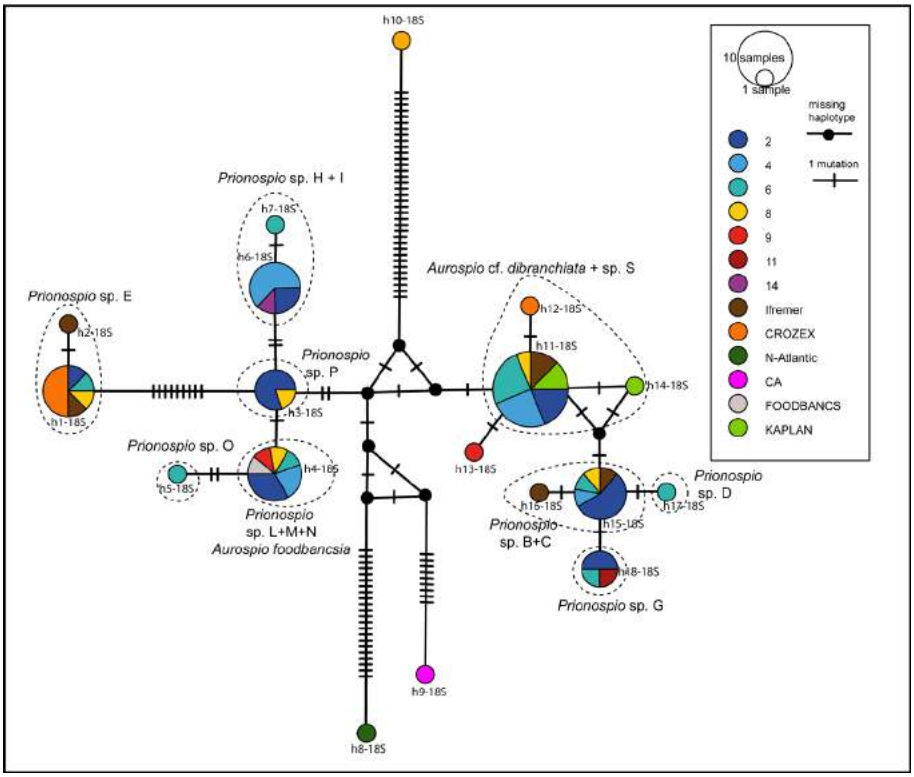

Figure 4. Genotype networks of Prionospio *and* Aurospio *species from the different localities of 18S gene fragments. Sampling localities are colour coded. Different lineages are circled.*

servative threshold for delimitating species, but this additional splitting would not change the main finding, concerning the dispersal potential of *Prionospio* and *Aurospio* (see below).

Unfortunately, our previous morphology-based species identification of the *Prionospio* and *Aurospio* specimens from the tropical Atlantic (Guggolz et al. 2018) showed high inconsistencies with the results presented here regarding the number of species. The assignment to genera showed consistency with the molecular results, but the number of species had been underestimated with morphological identification (Guggolz et al., 2018: eight *Prionospio* species, one *Aurospio* species). As all of the studied specimens were damaged and important species discriminating characters were often missing, morphological identification was limited, which could explain this inconsistency. The problem of morphological identification is known for deep-sea polychaetes, due to their soft bodies resulting in easy fragmentation and the way of sampling infauna from deep-sea sediments, where extreme care must be taken regarding sieving techniques to preserve morphology (Guggolz et al. 2019; Bogantes et al. 2018; Glover et al. 2016a). Furthermore, *Prionospio* and *Aurospio* are classified within the *Prionospio* complex, in which the generic characters are limited and still under debate (Paterson et al. 2016; Wilson 1990; Sigvaldadottir 1998; Yokoyama 2007). Especially, the taxonomic boundaries of *Prionospio* and *Aurospio* are problematic, as the main distinguishing feature is the beginning and shape of the branchiae, which has been suggested to be insufficient to discriminate the genera (Paterson et al. 2016; Wilson 1990; Sigvaldadottir 1998). The 16S phylogeny of the present work highlights this difficulty as both, *Prionospio* and *Aurospio* were found to be paraphyletic. For *Aurospio* sp. Q and sp. R only single sequences each were available from GenBank and these could have been misidentified (Collins and Cruickshank 2013; Kvist et al. 2010). However, even if this potential bias is considered also the relationships of *Aurospio foodbancsia* does not support monophyly of *Aurospio* (*Aurospio* cf. *dibranchiata*, *A*. sp. S and sp. T). As all of these species cluster within *Prionospio* in the 16S analyses and shared a genotype with *Prionospio* species in 18S also the monophyly of *Prionospio* is questionable. The morphological assignment of *A. foodbancsia* to the genus *Aurospio* is mainly based on the beginning of the branchiae (Mincks et al. 2009), which highlights again the limitation of the generic characters, delimitating the two genera from each other and emphasises the importance of molecular analyses within the *Prionospio* complex. To resolve these problems, there is a need for broad taxon sampling and a taxonomic revision including morphological and molecular characters.

Irrespective of the taxonomic status of *Prionospio* and *Aurospio*, the dataset presented here provides profound insights into the diversity of these genera in the deep sea. In the samples for the tropical Atlantic studied herein, spionids were a dominant faunal component with more than 73 % of all sampled polychaetes (Guggolz et al. 2018). The potential 19 deep-sea species (excluding the two GenBank entries *Aurospio* sp. Q and R) make up around 17 % of the worldwide described *Prionospio* and *Aurospio* species (around 108 species listed in WoRMS http://www.marinespecies.org/, Read and Fauchald 2018), keeping in mind that we cannot say for sure whether they represent species new to science or already described species. Our findings support previous reports that both genera are abundant in the deep sea, and presumably the number of species is still underestimated (Paterson et al. 2016).

One of the main aims of this study was to get an idea of the dispersal potential of the studied species. Some species were found to be restricted to one of the investigated oceans (*Prionospio* sp. C, D, F, G, I, K, L, M, O, P and *Aurospio* sp. T; Figs. 2, 3), but there are also several species found to have a pan-oceanic distribution (*Prionospio* sp. A, B, E, H, N and *Aurospio* cf. *dibranchiata*, sp. S; Figs. 2, 3). Most of these species found in the Atlantic, as well as in the Pacific show comparable patterns regarding the haplotype networks and thus of the distribution of their intraspecific genetic diversity. Identical haplotypes and genotypes are found in both oceans (h9-16S, h35-16S, h95-16S, h119-16S, h1-

18S, h8-18S, h12-18S; Figs. 3, 4), but there is still a degree of separation visible between the Atlantic and the Pacific, though often only based on one or a few mutations in 16S. Only *Prionospio* sp. A and sp. N seem to be more clearly separated genetically in the two oceans. These distinctions are also supported by the population analyses, which are revealing significant differences between the Pacific and Atlantic populations of selected species (*Prionospio* sp. B, H and *Aurospio* cf. *dibranchiata*, sp. S; Table 4). Despite these significant differences between the populations, we propose, based on the shared 16S haplotypes, that gene flow between the oceans is possible and occurs at times, but that gene flow rates are too low to lead to population admixture between oceans.

It is widely accepted that one of the main driving factors for such wide dispersal capacities of marine invertebrates are long-lived planktonic larval stages (Schüller and Ebbe 2007; Scheltema 1971; Rex et al. 2005; Eckman 1996; Yearsley and Sigwart 2011). Even if the specific type of larvae of the herein studied species is unknown, other species of *Prionospio* and *Aurospio* are reported to develop via planktonic larvae like other species of these genera (Blake et al. 2017; Mincks et al. 2009; Young 2004). The planktonic larval duration and dispersal distances are potentially higher in the deep sea, as the cold temperature and consequently reduced metabolic rates are identified as one of the main driving factors for extended larval stages (O'Connor et al. 2007; McClain and Hardy 2010). Considering the enormous distances between the CCZ and the VFZ, direct gene flow between the populations would be rather unlikely. It rather appears likely that the distribution over such large geographical distances is linked to ocean currents, connecting different suitable habitat patches in a stepwise fashion only (McClain and Hardy 2010; Young et al. 2008; Rex and Etter 2010). The direction of dispersal of *Aurospio* and *Prionospio* larvae remains unknown, as well as whether the species originate from the Pacific or the Atlantic. It seems highly unlikely that larvae drift all the way between the CCZ and the VTF. There are probably additional populations in the un-sampled regions. Dispersal could then be achieved stepwise via stepping stones. Further comparison to populations from other localities would help to clarify these issues. The potential to find conspecific specimens in other deep-sea areas that are potentially habitat patches or stepping stones, connecting the populations is supported by specimens from the Crozet Islands (Antarctica) that were assigned to *Prionospio* sp. E. This would also support the suggestion that the Southern Ocean is connecting the Atlantic and the Pacific most likely with the eastwards flowing deep-water currents (Stow et al. 2002; Rahmstorf 2002).

A pan-oceanic distribution found for *Aurospio* and *Prionospio* species as evidenced from molecular data, is so far unique for abyssal annelids, even if wide distribution ranges of polychaete species are not unusual (Guggolz et al. 2019; Meißner et al. 2016; Schüller and Hutchings 2012; Böggemann 2016; Eilertsen et al. 2018; Georgieva et al. 2015). However, Hutchings and Kupriyanova (2018) are particularly highlighting that reported "cosmopolitan" species should be treated with caution. For some species wide distribution ranges have been based on misidentification or cryptic species and subsequently rejected using molecular marker (Álvarez-Campos et al. 2017; Sun et al. 2016). The assumption that planktonic larvae in the deep sea are staying longer in the water column and transported via currents successfully over long distances raises the question of what the potential dispersal barrier restricting the distribution are? Definitely, different life-history traits like larval behavior, larval mortality and physiological tolerances for vertical movement and settlement in different habitats are important (McClain and Hardy 2010; Virgilio et al. 2009; Glover et al. 2001). It has been suggested that connectivity in the deep sea has often been associated with a common bathymetry rather than spatial vicinity (Glover et al. 2001). Thus, topographic barriers, like ridges, canyons and rises are supposed to influence distribution patterns (Guggolz et al. 2018; Eckman 1996; McClain and Hardy 2010; Won et al. 2003). Such a potential barrier is the MAR, dividing the Atlantic in eastern and western basins (Murray and Hjort 1912). Some of the

herein studied species (*Prionospio* sp. G, sp. L, sp. M and *Aurospio* cf. *dibranchiata*) occurring in the tropical Atlantic were found to be distributed across the MAR with wide distribution ranges of up to > 4,000 km (Fig.1, Fig. 3) with no or only little genetic differentiation between populations. Several haplotypes were found to be identical (h29-16S, h59-16S, h61-16S, h69-16S, h119-16S, h121-16S; Fig. 3), indicating gene flow across the MAR. Even for species restricted to one side of the MAR (eVFZ: *Prionospio* sp. H, sp. P and *Aurospio* sp. S) or at least to the VTF (*Prionspio* sp. B, sp. E, sp. N, sp. O), shared haplotypes were found across hundreds of kilometres (47-16S, h9-16S, h22-16S, h87-16S; Fig. 1, Fig. 3). These results are strongly refuting a barrier effect of the MAR for these *Prionospio* and *Aurospio* species. The dispersal potential across topographic barriers like the MAR and over large geographic distances was also reported recently for species of the spionid genus Laonice (Guggolz et al. 2019). The importance of dispersal via larvae is emphasized by distribution patterns found for brooding taxa like isopods, which exhibited very limited or no gene flow across the MAR (Bober et al. 2018; Brix et al. 2018).

In summary, the results of this study are expanding our knowledge of the diversity and distribution patterns of *Aurospio* and *Prionospio* in the deep sea. We could identify 21 lineages with some assigned to already described species (*Aurospio foodbancsia*, *Aurospio* cf. *dibranchiata*) and others remaining unknown at present. These other molecularly delineated potential species cannot be differentiated from described species, due to lack of sufficient morphological characters as most individuals were damaged and incomplete and because genetic data for most of the described species is lacking. The lack of monophyly for the two genera is highlighting the importance of molecular analyses additionally to morphological examinations to revise the *Prionospio* complex. A remarkable level of gene flow in some of the taxa was shown. The pan-oceanic distribution is indicating the potential of widespread distribution for *Prionospio* and *Aurospio* species, even over topographic/thermal barriers and should be kept in mind for further studies on distribution patterns in deep-sea polychaetes.

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Conflict of Interest

The authors declare no conflicts of interest.

References

Álvarez-Campos, P., Giribet, G., & Riesgo, A. (2017). The Syllis gracilis species complex: a molecular approach to a difficult taxonomic problem (Annelida, Syllidae). *Molecular phylogenetics and evolution*, 109, 138-150.

Bandelt, H. J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular biology and evolution*, 16(1), 37-48.

Bastrop, R., & Blank, M. (2006). Multiple invasions–a polychaete genus enters the Baltic Sea. *Biological Invasions*, 8(5), 1195-1200.

Bickford, D. et al. (2007). Cryptic species as a window on diversity and conservation. *Trends in ecology & evolution*, 22(3), 148-155.

Blake, J.A. & Kudenov, J. D. (1978). The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. Mem. *Memoirs of the National Museum of*

Victoria, 39, 171-280.

Blake, J. A., Maciolek, N. J. & Meißner, K. (2017) Spionidae Grube, 1850. In Schmidt-Rhaesa, A. (Ed.) *Handbook of Zoology, a Natural History of the Phyla of the Animal Kingdom—Annelida, Polychaetes* (pp. 1-109). De Gruyter.

Bober, S., Brix, S., Riehl, T., Schwentner, M., & Brandt, A. (2018). Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean?. *Deep Sea Research Part II: Topical Studies in Oceanography,* 148, 91-104.

Bogantes, V. E., Halanych, K. M., & Meißner, K. (2018). Diversity and phylogenetic relationships of North Atlantic *Laonice* Malmgren, 1867 (Spionidae, Annelida) including the description of a novel species. *Marine Biodiversity*, 1-13.

Böggemann, M. (2016) Glyceriformia (Annelida) of the abyssal SW Atlantic and additional material from the SE Atlantic. *Mariner Biodiversity* 46, 227–241.

Brasier M. J. *et al.,* (2016) DNA barcoding uncovers cryptic diversity in 50% of deep-sea Antarctic polychaetes. *Royal Society open science* 3, 160432.

Brix, S., Bober, S., Tschesche, C., Kihara, T.C., Driskell, A. & Jennings, R.M. (2018) Molecular species delimitation and its implications for species descriptions using desmosomatid and nannoniscid isopods from the VEMA fracture zone as example taxa. *Deep Sea Research Part II: Topical Studies in Oceanography,* 148, 180-207.

Caullery, M. (1914) Sur les polychètes du genre *Prionospio* Malmgren. *Bulletin de le Soci zoologique de France 39*, 355-361.

Cohen, B. L., Gawthrop, A. & Cavalier-Smith, T. (1998) Molecular phylogeny of brachiopods and phoronids based on nuclear- encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 353, 2039–2061.

Collins R. A. & Cruickshank, R. H. (2013) The seven deadly sins of DNA barcoding. *Molecular Ecology Resources,* 13, 969–75.

Dahlgren T. *et al.* (2016) Abyssal fauna of the UK-1 polymetallic nodule exploration area, Clarion-Clipperton Zone, central Pacific Ocean: Cnidaria. *Biodiversity Data Journal,* 4, e9277–31.

Devey, C.W. (2015) RV SONNE Fahrtbericht/Cruise Report SO237 Vema-TRANSIT: bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study, Las Palmas (Spain)-Santo Domingo (Dom. Rep.) 14.12.14 - 26.01.15.

Dzikowski, R., Levy, M.G., Poore, M.F., Flowers, J.R. & Paperna, I. (2004) Use of rDNA polymorphism for identification of Heterophyidae infecting freshwater fishes. *Diseases of aquatic organisms,* 59(1), 35-41.

Eckman, J. E. (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology,* 200(1), 207–237.

Eilertsen, M. H. *et al.* (2018) Genetic connectivity from the Arctic to the Antarctic: *Sclerolinum contortum* and *Nicomache lokii* (Annelida) are both widespread in reducing environments. *Scientific Reports*, 8(1), 4810.

Etter, R. J. *et al.* (2011) Phylogeography of a pan-Atlantic abyssal protobranch bivalve: implications for evolution in the Deep Atlantic. *Molecular Ecolology* 20.4, 829-843.

Excoffier, L. & Lischer, H.E. (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources,* 10(3), 564-567.

Foster, N. M. (1971) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Studies on the Fauna of Curaçao and other Caribbean Islands* 36(1), 1-183.

Funk, D. J. & Omland, K. E. (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics,* 34(1), 397-423.

Gallego, R., Lavery, S. & Sewell M. A. (2014) The meroplankton community of the oceanic Ross Sea during late summer. *Antarctic Science,* 26.4, 345-360.

Galtier, N., Nabholz, B., Glémin, S. & Hurst, G. D. D. (2009) Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecolology*, *18*(22), 4541-4550.

Georgieva, M. N., *et al.* (2015) A chemosynthetic weed: the tubeworm *Sclerolinum contortum* is a bipolar, cosmopolitan species. *BMC Evolutionary Biology,* 15.1, 280.

Glover, A. G., Paterson, G. L. J., Bett, B. J., Gage, J. D. & Sibuet, M. (2001) Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. *Deep-Sea Research Part I: Oceanographic Research Papers,* 48, 217–236.

Glover, A., Dahlgren, T., Wiklund, H., Mohrbeck, I. & Smith, C. (2016a) An end-to-end DNA taxonomy methodology for benthic biodiversity survey in the Clarion-Clipperton Zone, central Pacific abyss. *Journal of Marine Science and Engineering*, 4(1), 2.

Guggolz, T., Lins, L., Meißner, K. & Brandt, A. (2018) Biodiversity and distribution of polynoid and spionid polychaetes (Annelida) in the Vema Fracture Zone, tropical North Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography,* 148, 54-63.

Guggolz, T., Meißner, K., Schwentner, M. & Brandt, A. (2019) Diversity and distribution of *Laonice* species (Annelida: Spionidae) in the tropical North Atlantic and Puerto Rico Trench. *Scientific Rep*ort 9: 9260.

Halanych, K. M. & Janosik, A. M. (2006) A review of molecular markers used for Annelid phylogenetics. *Integrative and Comparative Biology,* 46, 533–543.

Hillis, D. M. & Dixon, M. D. (1991) Ribosomal DNA: molecular evolution and phylogenetic inference. *The Quarterly Review of Biology,* 66, 411–453.

Hutchings, P. & Kupriyanova, E. (2018) Cosmopolitan polychaetes–fact or fiction? Personal and historical perspectives. *Invertebrate Systematic*, *32*(1), 1-9.

Katoh, K. & Standley, D. M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. (outlines version 7). *Molecular Biology and Evolution,* 30, 772-780.

Kearse, M. *et al*. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28.12**, 1647-1649.

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution,* 33, 1870-1874.

Kvist, S., Oceguera-Figueroa, A., Siddall, M. E. & Erséus, C. (2010) Barcoding, types and the *Hirudo* files: Using information content to critically evaluate the identity of DNA barcodes. *Mitochondrial DNA,* 21, 198–205.

Linse, K. & Schwabe, E. (2018) Diversity of macrofaunal Mollusca of the abyssal Vema Fracture Zone and hadal Puerto Rico Trench, Tropical North Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography,* 148, 45-53.

Lodge, M. J. D., Le Gurun, G., Wengler, M., Weaver, P. & Gunn, V. (2014) Seabed mining: international seabed authority environmental management plan for the Clarion– Clipperton Zone. A partnership approach. *Marine Policy,* 49, 66–72.

Maciolek, N. J. (1981a) A new genus and species of Spionidae (Annelida: Polychaeta) from the north and south Atlantic. *Proceedings of the Biological Society of Washington,* 94, 228–239.

Maciolek, N. J. (1985) A revision of the genus *Prionospio* Malmgren, with special emphasis on species from the Atlantic Ocean, and new records of species belonging to the genera *Apoprionospio* Foster and *Paraprionospio* Caullery (Polychaeta, Annelida, Spionidae). *Zoological journal of the Linnean Society,* 84, 325–385.

Maciolek, N. J. (1981b) Spionidae (Annelida: Polychaeta) from the Galapagos Rift geothermal vents. *Proceedings of the Biological Society of Washington,* 94, 826–837.

Malmgren, A. J. (1867) Annulata Polychaeta Spetsbergiæ, Groenlandiæ, Islandiæ et Scandinaviæ. Hactenus Cognita. Ex Officina Frenckelliana, Helsingforslæ. 127.

Martínez-Arbizu, P. & Haeckel, M. (2015) RV SONNE Fahrtbericht/cruise report SO239: EcoResponse assessing the ecology, connectivity and resilience of polymetallic nodule field systems, Balboa (Panama) - Manzanillo (Mexico).

McClain, C. R. & Hardy, S. M. (2010) The dynamics of biogeographic ranges in the deep sea. *Proceedings of the Royal Society B: Biological Sciences, 277*(1700), 3533-3546.

McClain, C.R., Rex, M.A. & Etter, R.J. (2009) Deep-sea macroecology. In Witman, J.D., Roy, K. (Eds.) *Marine Macroecology* 65–100 (University of Chicago Press, Chicago, IL).

Medlin, L., Elwood, H. J., Stickel, S. & Sogin, M. L. (1998) The characterization of enzymatically amplified eukaryotic 16S-like rRNA-coding regions. *Gene* 71, 491–499.

Meißner, K., Bick, A., & Bastrop, R. (2011). On the identity of *Spio filicornis* (OF Müller, 1776)—with the designation of a neotype, and the description of two new species from the North East Atlantic Ocean based on morphological and genetic studies. *Zootaxa* **2815(1),** 1-27.

Meißner, K., Bick, A., & Götting, M. (2016). Arctic *Pholoe* (Polychaeta: Pholoidae): when integrative taxonomy helps to sort out barcodes. *Zoological journal of the Linnean Society*, 179(2), 237-262.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE)* 1-8. (New Orleans, LA).

Mincks, S.L., Dyal, P.L., Paterson, G.L.J., Smith, C.R. & Glover, A.G. (2009). A new species of *Aurospio* (Polychaeta, Spionidae) from the Antarctic shelf, with analysis of its ecology, reproductive biology and evolutionary history. *Marine Ecology* 30, 181–197.

Moritz, C. & Cicero, C. (2004). DNA barcoding: promise and pitfalls. *PLoS biology*, *2*(10), e354.

Murray, J. & Hjort, J. (1912). The Depths of the Ocean. (McMillan, London).

Nygren, A. & Sundberg, P. (2003). Phylogeny and evolution of reproductive modes in *Autolytinae* (Syllidae, Annelida). *Molecular Phylogenetics and Evolution,* 29, 235–249.

Nygren, A. *et al.* (2018). A mega-cryptic species complex hidden among one of the most common annelids in the North East Atlantic. *PloS one* 13.6, e0198356.

O'Connor, M. I. *et al.* (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences,* 104.4, 1266-1271.

Osborn, K. J., Rouse, G. W., Goffredi, S. K., & Robison, B. H. (2007). Description and relationships of *Chaetopterus pugaporcinus*, an unusual pelagic polychaete (Annelida, Chaetopteridae). *Biological Bulletin,* 212(1), 40-54.

Palumbi, S. R. *et al.* (1991). The Simple Fool's Guide to PCR, Version 2.0. Privately published, Univ. Hawaii.

Palumbi, S. R. (1996). Nucleic acids II: the polymerase chain reaction. In Moritz, C., Mable, B.K. (eds.) *Molecular Systematics* Hillis, 205–247 (Massachusetts: Sinauer & Associates Inc., Sunderland).

Paterson, G. L. J. *et al.* (2016). New *Prionospio* and *Aurospio* species from the deep sea (Annelida: Polychaeta). *Zootaxa* 4092.1, 1-32.

Priede, I.G. *et al.* (2013). Does presence of a mid-ocean ridge enhance biomass and biodiversity? *PLoS One,* 8 (5), e61550.

Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, 21(8), 1864-1877.

Rahmstorf, S. (2002). Ocean circulation and climate during the past 120,000 years. *Nature*, 419(6903), 207.

Rambaut A., Drummond A. J., Xie D., Baele G. & Suchard M.A. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology,* 67(5), 901-904

Read, G. & Fauchald, K. (Ed.) (2018). World Polychaeta database. *Prionospio* Malmgren, 1867. Accessed through: Glover, A.G., Higgs, N., Horton, T. World Register of Deep-Sea species.

Rex, M. A. *et al.* (2005). A sourcesink hypothesis for abyssal biodiversity. The *American Naturalist,* 165, 163–178.

Rex, M. A., & Etter, R. J. (2010). Deep-sea biodiversity: pattern and scale. (Harvard University Press).

Ronquist, F. & Huelsenbeck, J.P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics,* 19(12), 1572-1574.

Rousset, V., Pleijel, F., Rouse, G. W., Erséus, C. & Siddall, M. E. (2007). A molecular phylogeny of annelids. *Cladistics,* 23(1), 41-63.

Scheltema, R. S. (1971). Larval Dispersal as a Means of Genetic Exchange Between Geographically Separated Populations of Shallow-Water Benthic Marine Gastropods. *Biological Bulletin,* 140, 284–322

Schüller, M. & Ebbe, B. (2007). Global distributional patterns of selected deep-sea Polychaeta (Annelida) from the Southern Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography,* 54(16-17), 1737-1751

Schüller, M. & Hutchings, P. A. (2012). New species of Terebellides (Polychaeta: Trichobranchidae) indicate long-distance dispersal between western South Atlantic deep-sea basins. *Zootaxa* 3254, 1-31.

Sigvaldadottir, E. & Mackie, A. S. Y. (1993). *Prionospio steenstrupi*, *P. fallax* and *P. dubia* (Polychaeta, Spionidae): re-evaluation of identity and status. *Sarsia*, 78, 203–219

Sigvaldadottir, E. (1998). Cladistic analysis and classification of *Prionospio* and related general genera (Polychaeta, Spionidae). *Zoological Scripta*, 27, 175–187

Sjölin E., Erséus C. & Källersjö M. (2005). Phylogeny of Tubificidae (Annelida, Clitellata) based on mitochondrial and nuclear sequence data. *Molecular Phylogenetics and Evolution,* 35, 431–441.

Stamatakis A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics,* 30, 1312–1313

Stow, D. A., Faugères, J. C., Howe, J. A., Pudsey, C. J. & Viana, A. R. (2002). Bottom currents, contourites and deep-sea sediment drifts: current state-of-the-art. *Geological Society, London, Memoirs,* 22(1), 7-20

Struck, T. H., Nesnidal, M. P., Purschke, G., & Halanych, K. M. (2008). Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution,* 48(2), 628-645.

Sun, Y., Wong, E., Tovar-Hernandez, M., Williamson, J. & Kupriyanova, E. K. (2016). Is *Hydroides brachyacantha* (Serpulidae, Annelida) a widely-distributed species? *Invertebrate Systematic,* 30, 41–59.

Taylor, M. L. & Roterman, C. N. (2017). Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. *Molecular Ecology,* 26(19), 4872-4896.

Virgilio, M., Fauvelot, C., Costantini, F., Abbiati, M. & Backeljau, T. (2009). Phylogeography of the common ragworm *Hediste diversicolor* (Polychaeta: Nereididae) reveals cryptic diversity and multiple colonization events across its distribution. *Molecular Ecology*, 18(9), 1980-1994

Vrijenhoek, R. C. (2009). Cryptic species, phenotypic plasticity, and complex life histories: assessing deep-sea faunal diversity with molecular markers. *Deep Sea Research Part II: Topical Studies in Oceanography,* 56(19-20), 1713-1723.

Webster, H. E. (1879). The Annelida Chaetopoda of New Jersey. *Annual report on the New York State Museum of Natural History,* 32, 101-128.

Wiklund H. *et al.* (2017). Abyssal fauna of the UK-1 polymetallic nodule exploration area, Clarion-Clipperton Zone, central Pacific Ocean: Mollusca. *ZooKeys,* 707, 1–46

Wiklund H., Glover A. G., Johannessen P. J. & Dahlgren T. G. (2009). Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. *Zoological Journal of the Linnean Society,* 155, 774–785.

Wiklund, H., Neal, L., Dahlgren, T. G., Drennan, R., Rabone, M. & Glover, A. G. (Submitted). Abyssal fauna of polymetallic nodule exploration areas, eastern Clarion-Clipperton Zone, central Pacific Ocean: Annelida: Capitellidae, Opheliidae, Scalibregmatidae and Travisiidae.

Wilson, R.S. (1990). *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from southern Australia. *Memoirs of Museum Victoria,* 50, 243–274.

Wilson, W.H. (1991). Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science,* 48, 500–516.

Won, Y., Young, C. R., Lutz, R. A., & Vrijenhoek, R. C. (2003). Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: Bathymodiolus) from eastern Pacific hydrothermal vents. *Molecular Ecology,* 12(1), 169-184.

Yearsley, J. M., & Sigwart, J. D. (2011). Larval transport modeling of deep-sea invertebrates can aid the search for undiscovered populations. *PLoS One*, *6*(8), e23063

Yokoyama, H. (2007). A revision of the genus *Paraprionospio* Caullery (Polychaeta: Spionidae). *Zoological Journal of the Linnean Society,* 151(2), 253-284.

Young C.M. (2004). Reproduction, development and life-history traits. In Tyler, P.A. (ed.) *Ecosystems of the Deep Oceans* (pp. 381–426) (Elsevier, Amsterdam).

Young, C. R., Fujio, S. & Vrijenhoek, R. C. (2008). Directional dispersal between mid-ocean ridges: deep-ocean circulation and gene flow in *Ridgeia piscesae*. *Molecular Ecology,* 17.7, 1718-1731.

Supporting Information

Supplement 1. Specimens code, collection site, haplotype group, lineages/species and GenBank Accession numbers, deposit numbers and collection locations for all Prionospio and Aurospio specimens analysed in this study. GenBank Accession Numbers and museum registration Numbers will be given during publication.

Supplement 2. Phylogenetic tree of Prionospio and Aurospio specimens analysed in this study, based on the mitochondrial 16S gene fragment. Posterior probabilities shown next to the nodes (values below 0.8 are not shown); Bootstrap values are shown after slashes (values below 80 are not shown).

The Additional Supporting Information are not printed here due to their size. They can be downloaded as soon as the manuscript is accepted from the publishers website.

Author Contributions

First draft of the manuscript, analyses and figures were prepared by Theresa Guggolz. Polychaetes of the Vema-TRANSIT expedition were prepared and handled in the laboratory of the CeNak by Theresa Guggolz. Laboratory work on specimens from the CCZ was done by Paulo Bonifácio at the Ifremer Institute, France and Helena Wiklund at the Natural History Museum, London. Martin Schwentner and Karin Meißner were proof-reading the manuscript, giving advices for interpreting the data and helping with analyses of data. Angelika Brandt, Thomas Dahlgren, Paulo Bonifácio, Karin Meißner and Martin Schwentner were proof-reading the manuscript and giving advice for improving the content.

CHAPTER 6

Diversity, pan-oceanic and vertical distribution of deep-sea scale worms (Annelida: Polynoidae: *Bathypolaria*)

Manuscript

Diversity, pan-oceanic and vertical distribution of deep-sea scale worms (Annelida: Polynoidae: Bathypolaria)

Theresa Guggolz, Martin Schwentner and Angelika Brandt

Abstract

Bathypolaria Levenstein, 1981 (Annelida: Polynoidae) is a monotypic genus, belonging to the deep-sea subfamily Macellicephaline. Hitherto, the only described species *Bathypolaria carinata* Levenstein, 1981 is noted mainly known circumarctically. In this study, molecular markers (COI, 16S and 18S) are employed to study the diversity and distribution patterns of *Bathypolaria* specimens from the tropical Atlantic and the Puerto Rico Trench. For this purpose, different molecular analyses (Automated Barcode Gap Discovery, pairwise genetic distances, phylogenetics, haplotype networks) were used and recently reported *Bathypolaria* specimens from the Pacific were included. We were able to identify three main lineages and several sublineages, showing at least the potential for distribution ranges across topographic barriers like the Mid-Atlantic Ridge over 4,000 km with no or low genetic differentiation. Furthermore, a recent gene flow between extensive bathymetric ranges (> 4,000 m) was found, with *Bathypolaria* specimens from abyssal and hadal, sharing the same haplotypes. The results of this study are suggesting a unique dispersal potential of *Bathypolaria* species, especially in vertical movement, as well as an undiscovered diversity with at least two additional undescribed species belonging the genus *Bathypolaria*.

Introduction

Polynoidae, Kinberg, 1856, colloquially called scale-worms belong to a group of polychaetes, characterized by scales (elytra) covering the dorsum. The family is one of the most diverse polychaete taxa, regarding the number of genera and species (~900 species, ~167 genera; Read & Fauchald, 2018; Hutchings, 2000; Bonifácio & Menot, 2018). They occur in all marine benthic habitats, from shallow water to hadal trenches (e.g. Hartmann-Schröder, 1974; Fauchald, 1977, Hutchings, 2000; Wiklund et al., 2005). The majority of polynoids are free-living, but others are also known to build heavy mud tubes or are found as commensals with various invertebrates (Martin & Britayev, 1998). A variety of subfamilies within Polynoidae are supposed to be restricted to the deep sea. One of these deep-sea subfamilies is Macellicephalineae Hartmann-Schröder, 1971, compromising 95 species (Bonifácio & Menot, 2018). Many genera belonging to Macellicephalinae are monotypic, which has been suggested to indicate a high potential of undiscovered diversity of deep-sea polynoids (Bonifácio & Menot, 2018). One of these monotypic deep-sea genera is *Bathypolaria* Levenstein, 1981, composed of only one described species from the Canada Basin, *Bathypolaria carinata* Levenstein, 1981. *Bathypolaria carinata* was reported several times to occur circumarctically from depths around 1,500 – 3,200 m (Sirenko et al., 1996; MacDonald et al., 2010; Alalykina, 2018). Just recently, *B. carinata* was indentified morphologically in high abundance in the tropical Atlantic (~ 5,000 m depth) with an additional, potentially new species (*Bathypolaria* sp. 1: Guggolz et al., 2018). Furthermore, Bonifácio & Menot (2018) mentioned the presence of two species of *Bathypolaria* from the central Pacific (> 4,000 m depth), differentiated with molecular analyses, considering no possible differentiation of these two Pacific species from *Bathypolaria carinata*, as no molecular information is available for the type-species. Even though, these findings indicate a much more diverse and complex scenario regarding the diversity and distribution of this hitherto monotypic genus.

Unfortunately, appropriate morphological investigations of *Bathypolaria* species were found to be difficult, as the specimens are often in poor condi-

Table 1. Specimens code, haplotype group, lineages/species and GenBank Accession numbers, deposit numbers and collection locations for all *Bathypolaria* specimens analysed in this study. Detailed collection sites can be found in Supplement 1 in Guggolz et al., submitted B.

Station	genus	Spec. code	Lineage (sublineage) 16S	Lineage (sublineage) COI	GenBank no. (16S/ COI/18S)
6	*Bathypolaria*	145 I	---	B (B5)	
12	*Bathypolaria*	266 XVI	---	A (A1)	
4	*Bathypolaria*	130 I	A (A1)	---	
2	*Bathypolaria*	206	A (A1)	A (A1)	
13	*Bathypolaria*	234 III	A (A1)	---	
13	*Bathypolaria*	234	A (A1)	---	
12	*Bathypolaria*	235 I	A (A1)	---	
12	*Bathypolaria*	235 II	A (A1)	---	
12	*Bathypolaria*	235 III	A (A1)	---	
12	*Bathypolaria*	235 IV	A (A1)	---	
12	*Bathypolaria*	235	A (A1)	A (A1)	
13	*Bathypolaria*	236	A (A1)	A (A1)	
12	*Bathypolaria*	237 I	A (A1)	---	
12	*Bathypolaria*	237	A (A1)	A (A1)	
13	*Bathypolaria*	238 I	A (A1)	A (A1)	
13	*Bathypolaria*	238	A (A1)	A (A1)	
12	*Bathypolaria*	239 II	A (A1)	---	
12	*Bathypolaria*	239 III	A (A1)	---	
12	*Bathypolaria*	239 IV	A (A1)	A (A1)	
12	*Bathypolaria*	239	A (A1)	---	
12	*Bathypolaria*	240 I	A (A1)	---	
12	*Bathypolaria*	240 II	A (A1)	A (A1)	
12	*Bathypolaria*	240 IV	A (A1)	---	
12	*Bathypolaria*	240 V	A (A1)	---	
12	*Bathypolaria*	240 VI	A (A1)	---	
12	*Bathypolaria*	240	A (A1)	A (A1)	
12	*Bathypolaria*	241 I	A (A1)	A (A1)	
13	*Bathypolaria*	242	A (A1)	A (A1)	
2	*Bathypolaria*	246	A (A1)	---	
12	*Bathypolaria*	266 I	A (A1)	---	
12	*Bathypolaria*	266 II	A (A1)	---	
12	*Bathypolaria*	266 III	A (A1)	---	
12	*Bathypolaria*	266 IX	A (A1)	---	
12	*Bathypolaria*	266 VI	A (A1)	---	
12	*Bathypolaria*	266 VII	A (A1)	A (A1)	
12	*Bathypolaria*	266 VIII	A (A1)	A (A1)	
12	*Bathypolaria*	266 XI	A (A1)	---	
12	*Bathypolaria*	266 XII	A (A1)	---	
12	*Bathypolaria*	266 XIII	A (A1)	---	
12	*Bathypolaria*	266 XIX	A (A1)	A (A1)	
12	*Bathypolaria*	266 XV	A (A1)	A (A1)	
12	*Bathypolaria*	266 XVII	A (A1)	A (A1)	
12	*Bathypolaria*	266 XVIII	A (A1)	A (A1)	
12	*Bathypolaria*	266 XX	A (A1)	---	
12	*Bathypolaria*	266 XII	A (A1)	---	

Table 1 (continued)

Station	genus	Spec. code	Lineage (sublineage) 16S	Lineage (sublineage) COI	GenBank no. (16S/COI/18S)
12	*Bathypolaria*	266	A (A1)	---	
APEI-3	*Bathypolaria*	sp. 608	A (A2)	---	MH233176.1/---/MH233228 (Bonifácio & Menot, 2019)
APEI-3	*Bathypolaria*	sp. 608	A (A2)	---	MH233192.1 /---/--- (Bonifácio & Menot, 2019)
APEI-3	*Bathypolaria*	sp. 608	A (A2)	A (A2)	MH233175.1 /MH233268 /MH233227 (Bonifácio & Menot, 2019)
APEI-3	*Bathypolaria*	sp. 608	A (A2)	A (A2)	MH233177.1/MH23177/MH233229 (Bonifácio & Menot, 2019)
APEI-3	*Bathypolaria*	sp. 608	A (A2)	A (A2)	MH233193.1/MH233193/MH233241 (Bonifácio & Menot, 2019)
4	*Bathypolaria*	91	B (B1-5)	---	
2	*Bathypolaria*	122	B (B1-5)	B (B3)	
6	*Bathypolaria*	145 II	B (B1-5)	B (B2)	
6	*Bathypolaria*	145 III	B (B1-5)	---	
6	*Bathypolaria*	152	B (B1-5)	---	
8	*Bathypolaria*	170	B (B1-5)	---	
	Bathypolaria	173	B (B1-5)	B (B4)	
11	*Bathypolaria*	179	B (B1-5)		
Admundsen Sea, Southern Ocen	*Austropolaria*	*magnicirrata*	B (B6)	---	JX863896.1/---/JX863895.1 (Neal et al., 2012)
GSR	*Bathypolaria*	sp. 173	B (B1-5)	---	MH233154.1/---/MH233211 (Bonifácio & Menot, 2019)
IOM	*Bathypolaria*	sp. 173	B (B1-5)	---	MH233199.1/---/MH233245 (Bonifácio & Menot, 2019)
BGR	*Bathypolaria*	sp. 173	B (B1-5)	B (B1)	MH233151.1/MH233281/MH233206 (Bonifácio & Menot, 2019)
2	*Bathypolaria*	114	C	---	

tions and the type material seems to be lost (Bonifácio & Menot, 2018, Neal et al., 2012). Damages and fragmentation of deep-sea polychaetes during sampling procedures are known and often hampering morphological identification (Guggolz et al. 2019, submitted ; Bogantes et al., 2018, Glover et al., 2016). Hence, studies on diversity and distribution of deep-sea polychaetes are challenging and should be treated with caution, if solely based on morphology. Additional molecular analyses are a significant improvement (Guggolz et al. submitted; Glover et al., 2016; Bonifácio & Menot, 2018; Hutchings & Kupriyanova, 2018).

The main aim of this study is to investigate the diversity and distribution patterns of *Bathypolaria* from the Vema-Fracture-Zone (VFZ) and the Puerto Rico Trench (PRT). Recent studies have shown the potential for enormous widespread, even pan-oceanic distribution and rejected a potential barrier effect of the Mid-Atlantic-Ridge (MAR) on selected polychaetes from the VFZ (Guggolz et al., 2018, 2019, submitted). The herein studied genus *Bathypolaria* will be further reveal the dispersal potential of deep-sea species along the MAR and additionally give insights in depth distribution patterns of the genus, as specimens from abyssal and hadal

depths are included.

Material and Methods

Collection and identification of specimens

All newly studied *Bathypolaria* specimens were collected during the Vema-Transit Expedition from the tropical Atlantic and the Puerto Rico trench. More detailed information about sample treatment, sampling localities and initial identification are described in Guggolz et al. (2018, 2019, submitted), Devey et al. (2015) and Brandt et al. (2018).

DNA extraction, PCR amplification, sequencing and alignment

Extraction, amplification, sequencing and alignment are described in detail in Guggolz et al. (2019, submitted). Primers for the 16S, COI and 18S genes are listed in Guggolz et al. (2019, Table 2).

All in all, 63 specimens were successfully sequenced for 16S, 28 specimens for COI and 52 sequences for 18S.

Initial identification of species, phylogenetic analyses and haplotype networks

Automated Barcode Gap Discovery (ABGD), Bayesian phylogenetic analyses and computation of haplotype networks were performed as described in detail in Guggolz et al. (2019, submitted).

The phylogenetic analyses of the 16S and COI gene fragments were generated separately, as well as concatenated with the 18S gene fragments. Additionally available sequences of *Bathypolaria* and *Austropolaria magnacirrata* Neal et al., 2012 from GenBank were included (Table 1). *Austropolaria magnacirrata* was included in the study, as recent phylogenetic analyses are recovering the genus nested within *Bathypolaria* species (Bonifácio & Menot, 2018) As outgroup, a member of the same subfamily Macellicephalinae, *Hodor anduril*, Bonifácio & Menot, 2018, was chosen (Table 1).

Results

Alignment

The alignment of the 16S fragment included a total of 63 sequences with a minimum length of 491 base pairs (bp), with 136 bp being variable and 60 bp being parsimony informative. The COI alignment included 28 sequences with a minimum length of 658 bp, of which 253 bp were variable and 146 bp were parsimony informative. The alignment contained no indels and the derived amino acid consisted of 197 amino acids, with 22 variable positions and no stop codons. The alignment of the 18S fragment included a total of 52 sequences with a minimum length of 924 bp, of which only 24 bp were variable and 15 bp parsimony informative.

Species delimitation and diversity

The ABGD analysis of the COI dataset retrieved two lineages when barcode thresholds of 5.8 – 10 % were employed (*Bathypolaria* lineages A, B). Additionally yielded lineages with lower barcode thresholds will be treated as sublineages consequently. When lower barcode thresholds are employed for the COI dataset, additional sublineages were retrieved (5.1 – 5.6 % *Bathypolaria* lineages A1, A2; 0.5 – 4.9 %: *Bathypolaria* lineages A1, A2, B1, B2, B3, B4, B5). The ABGD analysis of the 16S dataset resulted in three lineages when barcode thresholds of 2.3 – 8.8 % were employed. Two of these lineages are in accordance with the two lineages retrieved for COI. However, the third lineage comprises a single specimen, which was only successfully sequenced for 16S and therefore missing in the COI analyses (Table 1: PVT 114). Consequently, these three lineages will be referred to as *Bathypolaria* lineage A - C and subsequently treated as main lineages (= putative species). Again, lower barcode thresholds resulted in additional sublineages (0.9 – 2.2 %) (*Bathypolaria* lineage A1, A2, B1-5, B6), whereby sublineage B6 is corresponding to a single individual (*Austropolaria magnacirrata*) from GenBank with no COI sequence available. Sublineage B1-5 was found as one sublineage in 16S and comprises the same individuals as the according sublineages differentiated for lineage B in COI. Pairwise genetic distances (uncorrected *p*-distances) between the main lineages (*Bathypolaria* lineage A - C) ranged for COI from

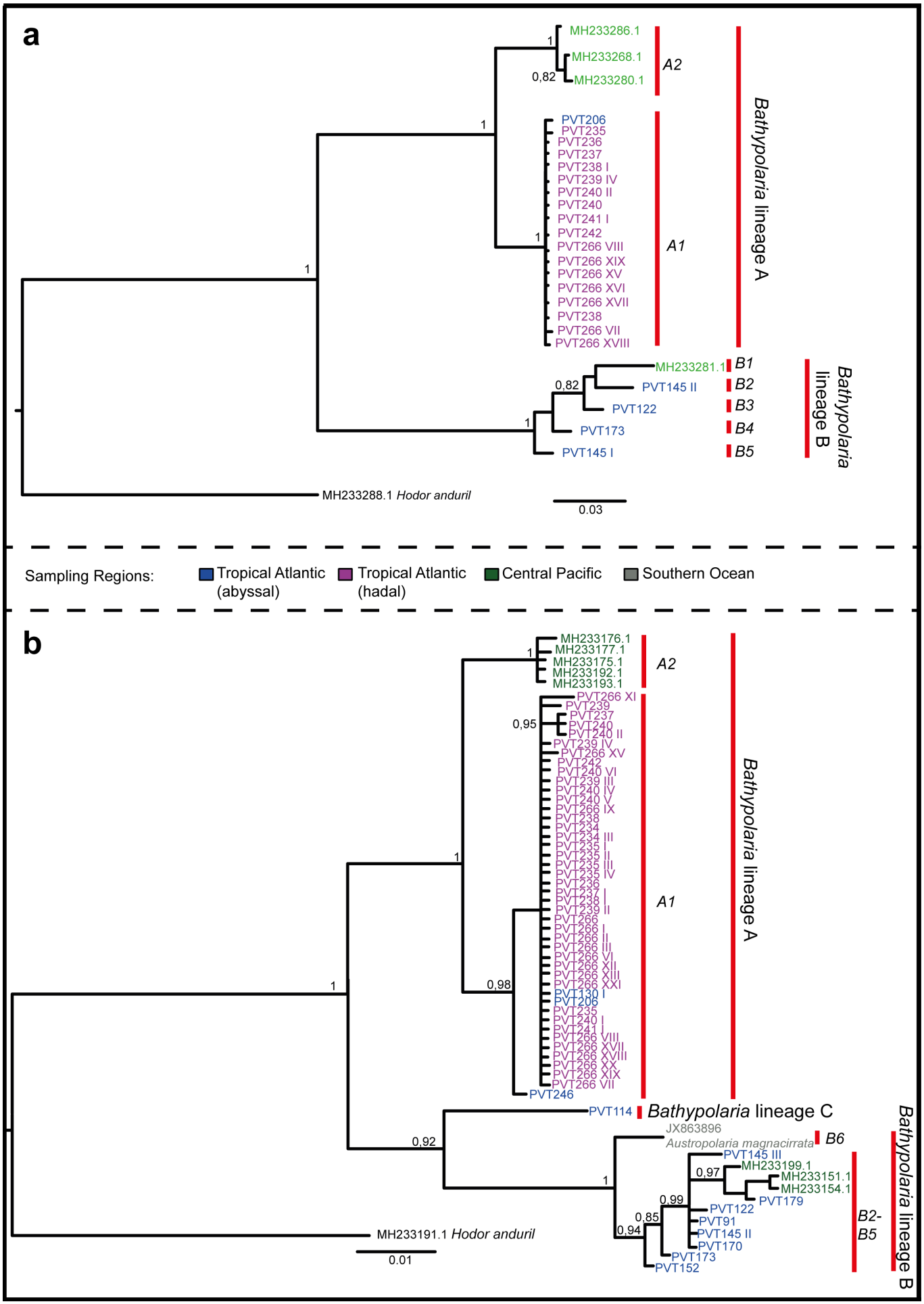

Figure 1. Phylogenetic tree of Bathypolaria lineages and sublineages obtained in the study based on mitochondrial COI (a) and 16S (b) gene fragments. Posterior probabilities shown next to the nodes (values below 0.8 are not shown). Individual occurrence in different oceans and depths is colour coded (see legend in the middle).

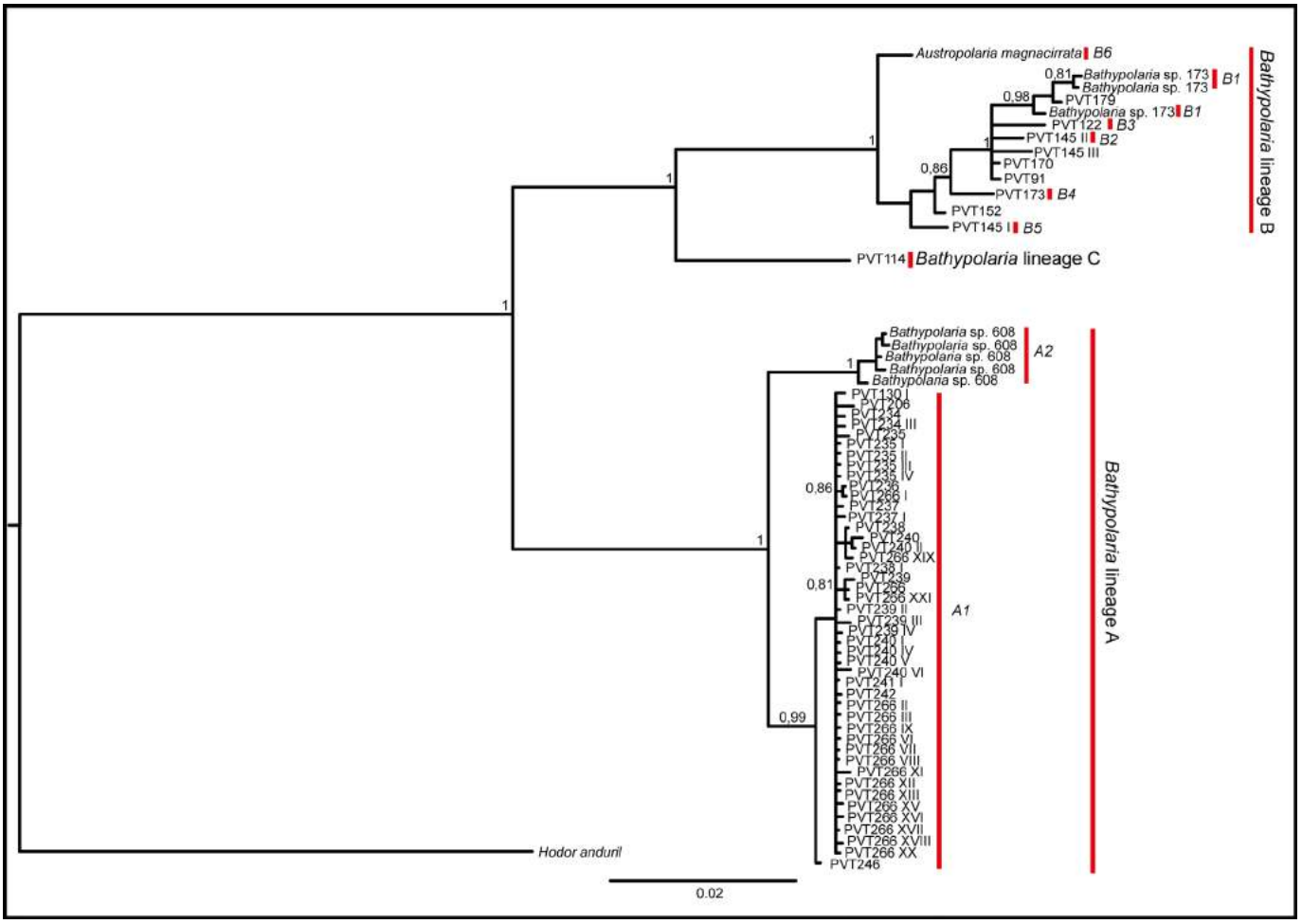

Figure 2. Concatenated phylogenetic tree (16S, COI and 18S) of Bathypolaria lineages and sublineages obtained in the study. Posterior probabilities shown next to the nodes (values below 0.8 are not shown).

17.6 – 19.5 %, for 16S from 7.3 – 12.7 % and for 18S from 0.1 – 1.3 % (Table 2). Intraspecific distances of the main lineages ranged for COI from 0 – 5.1 %, for 16S from 0 – 3.9 % and for 18S from 0 – 1.2 % (Table 2). Pairwise distances of the sublineages varied for 16S between A1 and A2 from 1.8 – 3.9 % and between B1-5 and B6 from 1.8 – 3.2 % (Table 3). For COI, pairwise distances between A1 and A2 ranged from 5.3 – 6.2 % (Table 3). Within the sublineages B1 – B5 the highest distance for COI was found between B4 and B5 (2.3 %) and the lowest distance was observed between sublineages B1 and B5 (5.1 %) (Table 3).

The phylogenetic analyses of 16S and COI, as well as the concatenated analyses of all three genes (16S, COI, 18S) recovered all three main lineages as reciprocal monophyletic with high or full support each (Fig. 1, 2). Also, the sublineages A1 and A2 were found as monophyletic with full support in all analyses (Fig. 1, 2). Within *Bathypolaria* lineage B, the sublineages were found in different relationships in the different phylogenetic analyses (Fig. 1, 2).

The haplotype networks of the three gene fragments

Table 2. Percentage of uncorrected p-distances within and among lineages for COI, 16S and 18S (see upper right corner). "X" means no or only one sequence available.

	Bathypolaria Lineage A	*Bathypolaria* Lineage B	*Bathypolaria* Lineage C
Bathypolaria Lineage A	0 – 3.9 0 – 6.2 0 – 1.2		16S COI 18S
Bathypolaria Lineage B	7.3 – 12.7 1.6 – 19.5 0.1 – 1.3	0 – 3.2 2.3 – 5.1 0 – 0.5	
Bathypolaria Lineage C	8.6 – 10.8 X X	6.9 – 7.7 X X	X X X

(16S, COI, 18S) showed comparable patterns. For

Table 3. Percentage of uncorrected p-distances within and among sublineages for COI and 16S (see upper right corner). "X" means no or only one sequence available. Grey shaded cells are marking sublineages that were delimited for only one of the gene fragments.

		Bathypolaria lineage A		*Bathypolaria* lineage B						
		A1	A2	B1	B2	B3	B4	B5	B1-5	B6
Bathypolaria lineage A	A1	0 - 0.8 0 - 0.5								16S COI
	A2	1.8 – 3.9 5.3 – 6.2	0 – 0.5 0 – 0.4							
Bathypolaria lineage B	B1	X 18.6 – 18.8	X 18.7 – 19.5	X X						
	B2	X 18 – 18.5	X 18.3 – 18.9	X 4.6	X X					
	B3	X 17.7 – 18.6	X 18.5 – 19.4	X 3.3	X 2.9	X X				
	B4	X 17.6 – 18.4	X 18.3 – 19.1	X 4.6	X 3.8	X 3.2	X X			
	B5	X 17.8 – 18.3	X 18.1 – 18.6	X 5.1	X 4.6	X 3.6	X 2.3	X X		
	B1-5	7.8 – 12.7 X	8.6 – 10.5 X						0 – 1.4 X	
	B6	8.6 – 9.2 X	8.2 – 10.6 X						1.8 – 3.2 X	X X
Bathypolaria lineage C		9.2 – 10.8 X	8.6 – 9 X						6.9 – 7.7 X	7.5 X

COI, with the lowest number of sequenced individuals, 12 were found with a maximum of 7 haplotypes in lineage A (Fig. 3a). For 16S, 18 haplotypes were found with a maximum of 9 haplotypes in lineage B (Fig. 3b). In the networks of both mitochondrial genes a differentiation with several mutations between the different sublineages can be observed (Fig. 3a, b), although the number of mutational steps between the sublineages are higher in the COI gene fragment (Fig. 3b). The 18S network showed a comparable diversity as in 16S and COI with a total of 18 genotypes. *Bathypolaria* lineages A and B can be differentiated from each other with no shared genotypes (Fig. 3c). Nothing can be stated about lineage C, as the single individual was only successfully sequenced for 16S (Fig. 3b).

For *Bathypolaria* lineages A and B a potential pan-oceanic distribution with occurrence in the Atlantic and the Pacific, as well as in the Southern Ocean for lineage B (16S) can be observed (Figs. 1, 3). However, the sublineages A1 and A2 are corresponding to either the Atlantic or the Pacific (Fig. 3a, b) respectively in both mitochondrial genes. Additionally, sublineage A1 is found to share haplo- and genotypes from individuals from abyssal (VFZ ~ 5,000 m) and hadal depths (PRT ~ 8,000 m) (Fig. 3) across geographic distances exceeding 4,000 km. In COI, no geographic allocation can be found for the sublineages B1–5 (Fig. 3a), but they are jointly retrieved as one sublineage in 16S with a shared haplotype between individuals from the VFZ and the Pacific or at least only few mutations (Fig. 3b). Furthermore, according to the sublineages B1-5 and B6 in 16S the specimen from the Southern Ocean is differentiated from the Pacific and tropical Atlantic specimens (Fig. 3b).

Discussion

Based on the mitochondrial 16S and COI fragments, comparable lineages were delimited. Three main lineages (*Bathypolaria* lineages A, B and C) could be identified well supported, whilst acknowledging that lineage C, comprising a single specimen (PVT114), was only successfully sequenced for 16S.

Even though, a potential splitting of the main lineages in several sublineages is found, the entirety of the results is strongly supporting the three main lineages A, B and C. The differentiation of the sublineages might be explained with the inclusion of specimens from large geographic sampling, resulting in different populations with partially high divergence between them (Guggolz et al., submitted). However, the three main *Bathypolaria* lineages should be more likely interpreted as putative species than the sublineages, as intraspecific distances were always lower than interspecific distances and the intraspecific distances of the three main lineages were still within the scope of intraspecific distances reported for other polychaetes species, which usually reach up to 5 – 6 % for both mitochondrial gene fragments (Kvist, 2010; Janssen et al., 2015; Mahon et al., 2009; Meißner & Blank, 2009; Meißner et al., 2016; Brasier et al., 2016; Álvarez-Campos et al., 2018; Guggolz et al., 2019, submitted).

Though, the three main lineages might not be interpreted unambiguous as three species, the 18S genotype network is also supporting the main lineages, as lineages A and B are clustering together subsequently and sublineages A1 and A2 are even sharing one genotype. Indeed, there is a surprising high diversity for the nuclear 18S gene as the same number of genotypes is found as haplotypes in 16S and even a higher number than in COI (Fig. 3a, b, c). Such diversity for 18S was not expected, because the gene is usually found to have a lower substitution rate than mitochondrial genes for metazoan (Halanych & Janosik, 2006; Hillis & Dixon, 1991). In both lineages the diversity is notably higher than found recently within polychaete species from the same area (Guggolz et al., A, B). Interestingly, in *Bathypolaria* lineage A, the majority of the diversity found for the 18S gene within this lineage is represented by specimens from the hadal tropical Atlantic in the PRT. This could be an indication for a more ancient population of *Bathypolaria* lineage A in the PRT compared to the populations from the Pacific and the abyssal tropical Atlantic.

Unfortunately, a delimitation of the potential *Bathypolaria* species based on morphology (Guggolz et al., 2018) shows high inconsistency with the herein presented results. Guggolz et al. (2018) proposed two *Bathypolaria* species, both showing high similarities to the type species *Bathypolaria carinata,* like the ventral keel at the posterior end, the number of segments (15) and the number of pairs of reduced elytrophores (8) (Levenstein, 1981). Specimens from the PRT were found to have slightly morphological differences to *Bathypolaria carinata*, like the position of the median antennae (placed more anteriorly, near median notch) and the shape of the neuropodium (more rectangular than described for *B. carinata*). The differentiation between *Bathypolaria* specimens from the abyssal and the hadal tropical Atlantic could not be confirmed with the herein presented molecular results. The morphological differences might be explained rather with damages caused by sampling procedure and fixation than real discriminating characters. The challenges in appropriate morphological identification of deep-sea polychaetes caused by their soft-body, often damaged or fragmented during the recovery from these depths is known (Bogantes et al., 2018; Guggolz et al., 2018, 2019, submitted; Glover et al., 2016). This seems to be also the case for *Bathypolaria*, as it is described to show typical morphological adaptations to deep-sea environments like delicate elytra, relatively thin and long chaetae and exceptionally long dorsal cirri (Uschakov, 1982), which are easily lost or damaged during sampling procedures (Bonifácio & Menot, 2018). Bonifácio and Menot (2018) recently mentioned two species of *Bathypolaria* from the Pacific with molecular methods, but due to the described difficulties with morphological characters, they were not able to make an adequate taxonomic description. These two species of *Bathypolaria* are found

within two of the main lineages (A and B) in this study, corresponding to sublineages A2, B1 and B1-5 (Fig. 1, 2, 3; Table 1).

Interestingly, the type specimen of *Austropolaria* was found to be closely related with the herein studied *Bathypolaria* specimens. *Austropolaria* was described as new genus differentiated from *Bathypolaria* based on the higher number of segments (20) and the higher number of pairs of reduced elytrophores (9) (Neal et al., 2012). None of the herein studied specimens, where morphological investigations were possible, were found to have the number of segments and reduced elytrophores described for *Austropolaria*. Consequently, the results of this study cast doubts about the generic characters, delimitating both genera and a morphological and molecular revision could help to clarify the status of *Austropolaria*.

As already mentioned, all herein studied specimens share generic characters with *Bathypolaria carinata,* the only described species in the genus (number of segments, ventral keel and flattened notochaeta), but it is not possible to explicitly distinguish them from each other based on morphology. Though, based on the herein presented results, we propose at least the presence of two additional undescribed species for the genus from the tropical Atlantic and the Pacific.

Despite the number and identification of species, new insights about the distribution patterns of *Bathypolaria* can be found. As already mentioned initially, *Bathypolaria* was thought to be monotypic and restricted to abyssal circumarctic regions so far (Sirenko et al., 1996; MacDonald et al., 2010; Alalykina, 2018; Levenstein, 1981). The herein studied specimens from the tropical Atlantic, the Pacific and the Southern Ocean are indicating a more global and cosmopolitic distribution pattern. It is proposed that one main driving factor for the dispersal potential of marine invertebrates is the development via planktonic larvae, distributed through water currents (Scheltema, 1971; Rex, 2005; Eckman, 1996; Yearsley & Sigwart, 2011). Even though, the exact mode of development is unknown for *Bathypolaria*, Polynoidae are usually reported to have planktonic larval stages (Hutchings, 2000), which is a strong indication for *Bathypolaria* to also bear planktonic larvae. Furthermore, *Bathypolaria carinata* was observed to be able to swim (McDonald et al., 2010). This high mobility is proposed to be supported by certain morphological features of the genus, like the exceptional long dorsal cirri (Bonifácio & Menot, 2018). Consequently, the genus seems to have a great potential for wide geographical distributions.

Based on the herein presented results a pan-oceanic dispersal potential appears possible, even if there seems to be an apparent separation of the populations, regarding the sublineages according with the different oceans respectively. At least, the MAR is most likely no barrier for the dispersal of *Bathypolaria* specimens, as shared haplo- and genotypes are observed between the PRT and the eastern most part of the VFZ (~ 4,000 km).

The potential to distribute over large geographic distances and across topographic barriers like the MAR was recently found for different spionid genera from the VFZ (Guggolz et al., 2019, submitted), but in contrast to *Bathypolaria* specimens, some populations of the studied *Prionospio* Malmgren, 1867 and *Aurospio* Maciolek, 1981 species were found to be less differentiated between the tropical Atlantic and the Pacific (Guggolz et al., submitted). These spionids are also proposed to have such wide dispersal capabilities based on planktonic larval stages (Guggolz et al., submitted), but in contrast to the high motility of adult *Bathypolaria* specimens, *Prionospio* and *Aurospio* are tube dwellers with limited motility (Jumars et al., 2015). The potentially wider and more successful horizontal dispersal capacities of the spionids, although they are less mobile as adults than *Bathypolaria,* are further supporting the importance of larval development for the distribution of deep-sea polychaetes.

One of the most remarkably results is that some of the herein studied *Bathypolaria* specimens show an enormous range of vertical distribution, as specimens with no genetic differentiation over nearly 4,000 m depth differences (Brandt et al., 2018) were found. Shared haplotypes (in 16S and 18S)

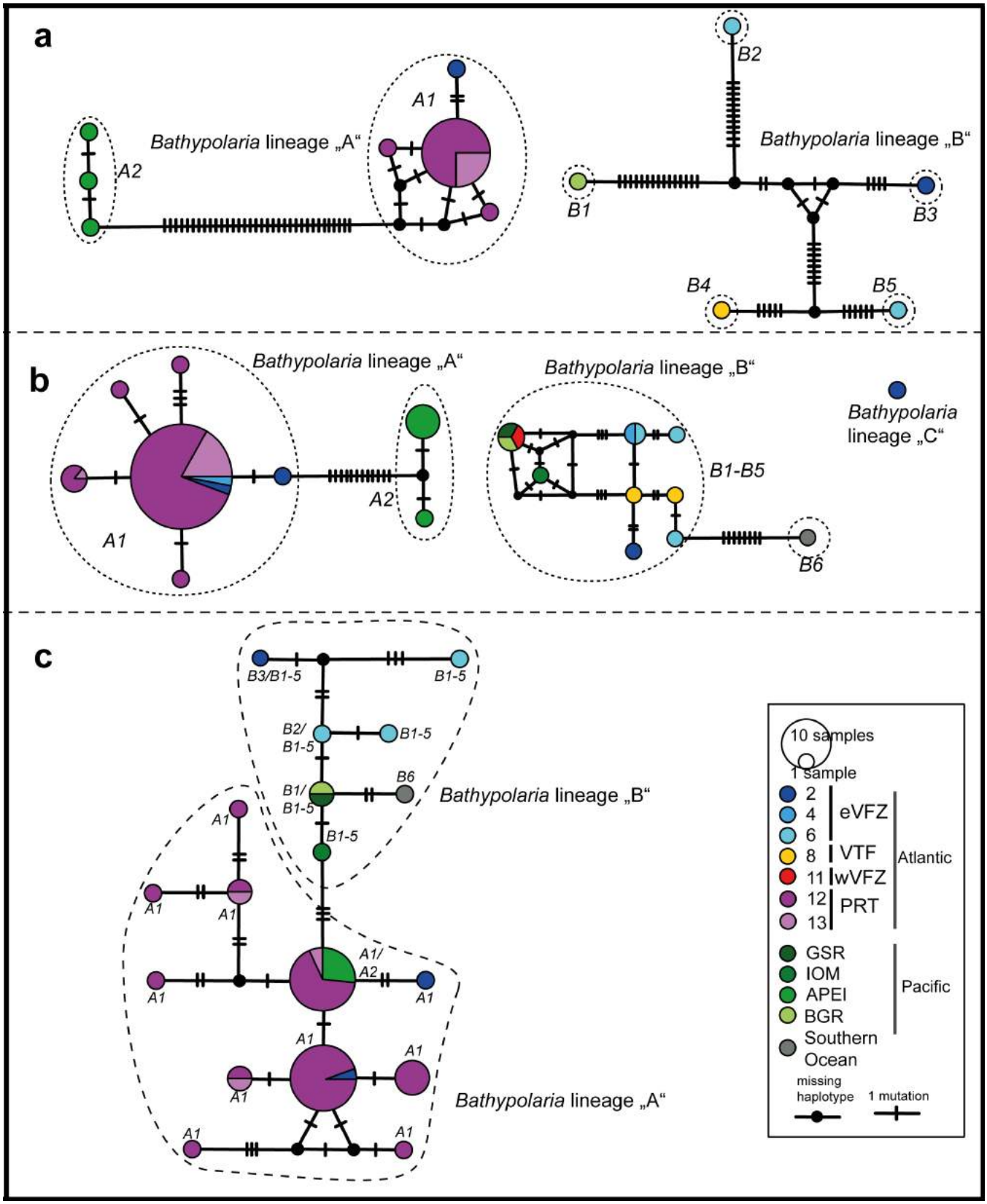

Figure 3. Haplo- and genotype networks of Bathypolaria lineages from the different localities of COI (a),16S (b) and 18S (c) gene fragments. Lineages (c) and sublineages (a, b) are marked with circles. Sampling localities are colour coded.

or at least only few mutations (in COI) between the hadal PRT and the abyssal VFZ can be observed within lineage A (sublineage A1). These results are a strong indication for an ongoing gene flow in *Bathypolaria* between the abyssal tropical Atlantic and the hadal PRT. This is quite unique, as such eurobathic distribution was never reported before for deep-sea polychaetes. Usually, a general pattern is proposed that vertical divergence between deep-sea populations is far greater than horizontal divergence over similar scales (Taylor & Roterman, 2017, Guggolz et al. submitted). Furthermore, hadal trenches are commonly described as highly endemic and isolated, promoting allopatric speciation

caused by depth and originating in the surrounding abyssal (Jamieson, 2015). Only few invertebrates, mainly arthropods and holothurians are recorded with comparable bathymetric ranges (> 4,000 m) (Belyaev, 1989; Jamieson, 2015). The vertical pressure gradient is supposed to be one of the main driving factors for the isolation of trenches (Fujii et al., 2013; Jamieson, 2015). *Bathypolaria* species seems to have a special physiological tolerance for vertical movement, as no or only small differentiation between the hadal and abyssal populations was found. It might be a taxon-specific adaption for successful settling in an environment like a hadal trench. This assumption is supported by the significant high abundance of *Bathypolaria* in polychaete samples from the PRT (unpublished data).

The herein presented results are indicating an undiscovered diversity for the so far monotypic deep-sea genus *Bathypolaria*. We suggest higher sampling efforts with appropriate gears like epibenthic sledges, which can help to catch such mobile epibenthic taxa (Bonifácio & Menot, 2018) and subsequent appropriate careful sampling treatment (Glover et al., 2016) would significantly help to expand the knowledge about this taxon. The presented results are indicating a particularly interesting distribution pattern for the genus *Bathypolaria*, with rather successful vertical as well as horizontal movement. Thus, these distribution patterns are emphasizing a complex scenario influencing dispersal potential of deep-sea polychaetes, which could help to further understand the driving mechanisms in the deep sea.

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References

Alalykina, I. L. Composition of deep-sea polychaetes from the SokhoBio expedition with a description of a new species of *Labioleanira* (Annelida: Sigalionidae) from the Sea of Okhotsk. *Deep-Sea Res. Pt II* **154,** 140-158 (2018).

Álvarez-Campos, P., Giribet, G. & Riesgo, A. The *Syllis gracilis* species complex: a molecular approach to a difficult taxonomic problem (Annelida, Syllidae). *Mol. Phylogenetics Evol.* **109,** 138–150 (2017).

Ansell, A. D., et al. Symbiotic polychaetes: review of known species. *Oceanogr. Mar. biol*. **36**, 217-340 (1998).

Belyaev, G.M. Deep-sea Ocean Trenches and Their Fauna. (Moscow: Nauka, 1989).

Bogantes, V.E., Halanych, K.M. & Meißner, K. Diversity and phylogenetic relationships of North Atlantic *Laonice* Malmgren, 1867 (Spionidae, Annelida) including the description of a novel species. *Mar. Biodivers*. **1-13** (2018).

Bonifácio, P. & Menot, L. New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida). *Zool. J. Linn. Soc.* **185.3,** 555-635 (2018):

Brandt, A., et al. Composition of abyssal macrofauna along the Vema Fracture Zone and the hadal Puerto Rico Trench, northern tropical Atlantic. *Deep-Sea Res. Pt II* **148**, 35-44 (2018).

Brasier M. J. et al., DNA barcoding uncovers cryptic diversity in 50% of deep-sea Antarctic polychaetes. *R. Soc. open Sci.* **3,** 160432 (2016).

Devey, C.W. RV SONNE Fahrtbericht/Cruise Report SO237 Vema-TRANSIT: bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study, Las Palmas (Spain)-Santo Domingo (Dom. Rep.) 14.12.14 - 26.01.15 (2015).

Eckman, J. E. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *J. Exp. Mar. Biol. Ecol*. **200(1),** 207–237 (1996).

Fujii, T., Kilgallen, N. M., Rowden, A. A., & Jamieson, A. J. Deep-sea amphipod community structure across abyssal to hadal depths in the Peru-Chile and Kermadec trenches. *Mar Ecol Prog Ser,* **492**, 125-138 (2013).

Glasby, C.J., Hutchingsen, P.A., Fauchald, K., Paxton, H., Rouse, G.W. Watson Russell, C., Wilson, R.S. Class polychaeta in: *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia*. pp. 1–296. (CSIRO Publish-

ing, Melbourne, 2000).

Glover, A., Dahlgren, T., Wiklund, H., Mohrbeck, I. & Smith, C. An end-to-end DNA taxonomy methodology for benthic biodiversity survey in the Clarion-Clipperton Zone, central Pacific abyss. *J. Mar. Sci. Eng*., **4(1),** 2 (2016).

Guggolz, T., Lins, L., Meißner, K. & Brandt, A. Biodiversity and distribution of polynoid and spionid polychaetes (Annelida) in the Vema Fracture Zone, tropical North Atlantic. *Deep-Sea Res. Pt II* **148,** 54-63 (2018).

Guggolz, T., Meißner, K., Schwentner, M. & Brandt, A. Diversity and distribution of *Laonice* species (Annelida: Spionidae) in the tropical North Atlantic and Puerto Rico Trench. *Sci. Rep.* 9: 9260 (2019).

Guggolz, T.,Meißner, K.,Schwentner, M., Dahlgren, T.G., Wiklund, H. & Brandt, A. High diversity and pan-oceanic distribution of deep-sea polychaetes: *Prionospio* and *Aurospio* (Annelida: Spionidae) in the Atlantic and Pacific Ocean. *Org. Divers. Evol.* Submitted.

Halanych, K. M. & Janosik, A. M. A review of molecular markers used for Annelid phylogenetics. *Integ. Comp. Biol.* **46**, 533–543 (2006).

Hartmann-Schröder G. Die Unterfamilie Macellicephalinae Hartmann-Schröder, 1971 (Polynoidae, Polychaeta). Mit Beschreibung einer neuen Art, *Macellicephala jameensis* n. sp., aus einem Höhlengewässer von Lanzarote (Kanarische Inseln). *Mitt. Hamb. Zool. Mus. Inst*. **71,** 75–85 (1974).

Hartmann-Schröder, G. Teil 58. Annelida, Borstenwürmer, Polychaeta. In: *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* (eds. Dahl M, Peus F.) 1–594 (Stuttgart: Gustav Fischer Verlag Jena, 1971).

Hillis, D. M. & Dixon, M. D. Ribosomal DNA: molecular evolution and phylogenetic inference. *Q. Rev. Biol.* **66**, 411–453 (1991).

Hutchings, P. & Kupriyanova, E. Cosmopolitan polychaetes–fact or fiction? Personal and historical perspectives. *Invertebr. Syst.,* **32(1),** 1-9 (2018).

Jamieson, A. The hadal zone: life in the deepest oceans. (Cambridge University Press, 2015)

Janssen, A., Kaiser, S., Meißner, K., Brenke, N., Menot, L., Martínez Arbizu, P. A reverse taxonomic approach to assess macrofaunal distribution patterns in abyssal pacific polymetallic nodule fields. *PLoS One* **10:e0117790** (2015).

Jumars, P. A., Dorgan, K. M. & Lindsay, S. M. Diet of worms emended: an update of polychaete feeding guilds. *Annu. Rev. Mar. Sci.* **7,** 497-520 (2015).

Kvist, S., Oceguera-Figueroa, A., Siddall, M. E. & Erséus, C. Barcoding, types and the Hirudo files: Using information content to critically evaluate the identity of DNA barcodes. *Mitochondrial DNA* **21,** 198–205 (2010).

Levenstein, R.Y.A. Some peculiarities of the distribution of the family Polynoidae from the Canada basin of the Arctic Ocean. *Tr. Inst. Okeanol. im. P. P. Shirshova, Akad. Nauk SSSR*, **115,** 26–36 (1981).

MacDonald, I. R., et al. Benthic macrofauna and megafauna assemblages in the Arctic deep-sea Canada Basin. *Deep-Sea Res. Pt II* **57**.1-2, 136-152 (2010).

Maciolek, N. J. A new genus and species of Spionidae (Annelida: Polychaeta) from the north and south Atlantic. *Proc. Biol. Soc. Wash.* **94,** 228–239 (1981).

Mahon, A.R., Mahon, H.K., Dauer, D.M., Halanych, K.M. Discrete genetic boundaries of three *Streblospio* (Spionidae, Annelida) species and the status of *S. shrubsolii*. *Mar. Biol. Resear*. **5,** 172–178 (2009).

Malmgren, A. J. Annulata Polychaeta Spetsbergiæ, Groenlandiæ, Islandiæ et Scandinaviæ. Hactenus Cognita. Ex Officina Frenckelliana, Helsingforslæ. **127** (1867).

Meißner, K., Bick, A., & Götting, M. Arctic *Pholoe* (Polychaeta: Pholoidae): when integrative taxonomy helps to sort out barcodes. *Zool. J. Linn. Soc,* **179(2),** 237-262 (2016).

Meißner, K., Blank, M. *Spiophanes norrisi* sp. nov. (Polychaeta: Spionidae) a new species from the NE Pacific coast, separated from the *Spiophanes bombyx* complex based on both morphological and genetic studies. *Zootaxa* **2278,** 1–25. (2009).

Neal, L., Barnich, R., Wiklund, H., & Glover, A. G. A new genus and species of Polynoidae (Annelida, Polychaeta) from Pine Island Bay, Amundsen Sea, Southern Ocean-a region of high taxonomic novelty. *Zootaxa*, (**3542),** 80-88 (2012).

Read G., Fauchald K. World Polychaeta database. Polynoidae Kinberg, 1856. World Register of Marine Species. Available at: http://www.marinespecies.org/aphia.

php?p=taxdetails&id=939 (2018).

Rex, M. A. et al. A sourcesink hypothesis for abyssal biodiversity. *Am. Nat.* **165,** 163–178 (2005).

Scheltema, R. S. Larval Dispersal as a Means of Genetic Exchange Between Geographically Separated Populations of Shallow-Water Benthic Marine Gastropods. *Biol. Bull.* **140,** 284–322 (1971)

Sirenko, B. I., et al. Preliminary data on suprabenthic invertebrates collected during the RV Polarstem cruise in the Laptev Sea. *Polar Biol.* **16.5,** 345-352 (1996).

Taylor, M. L. & Roterman, C. N. Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. *Mol. Ecol*. **26(19),** 4872-4896 (2017).

Uschakov, P. V. Polychaetes of the suborder Aphroditiformia of the Arctic Ocean and the northwestern part of the Pacific Ocean. Families Aphroditidae and Polynoidae. Mnogoshchetinkovyye Chervil (Fauna of the USSR, Polychaeta) **2,** 1–272 (1982).

Wiklund, H., et al. Phylogeny of Aphroditiformia (Polychaeta) based on molecular and morphological data. *Mol. Phylogenetics Evol.* **37.2,** 494-502 (2005).

Yearsley, J. M., & Sigwart, J. D. Larval transport modeling of deep-sea invertebrates can aid the search for undiscovered populations. *PLoS One*, **6(8),** e23063 (2011).

Author Contributions

First draft of the manuscript, analyses and figures were prepared by Theresa Guggolz. Polychaetes of the Vema-TRANSIT expedition were prepared and handled in the laboratory of the CeNak by Theresa Guggolz. Martin Schwentner was proof-reading the manuscript, giving advices for interpreting the data and helping with analyses of data. Angelika Brandt was the head of the expedition and initiated the Vema-TRANSIT project and additionally proof-reading the manuscript.

CHAPTER 7

General Discussion

General Discussion

I. Biodiversity of deep-sea polychaetes

Polychaetes are usually one of the most abundant groups found within the benthic deep-sea macrofauna (e.g. Gage and Tyler 1992, Grassle and Maciolek 1992, Glover et al. 2001, Fiege et al. 2010). This was also the case in the samples obtained during the Vema-Transit Expedition, with polychaetes being the second most abundant group after crustaceans representing ~24 – 26 % of the total macrofauna (Table 1; Chapter 2, 3). This proportion is slightly lower than the sometimes reported relative abundances for polychaete, which can make up half of the total number of individuals (e.g. Gage and Tyler 1992, Fiege et al. 2010). However, when comparing such abundance data, the used gears have to be considered. Different gears (e.g. box corer, Agassiz trawls, epibenthic sledges) can affect the sampled taxa, as for instance mobile or very small individuals can be missed (see Discussion Chapter 2). Additionally, the epibenthic sledge, used during the Vema-TRANSIT expedition, is known to be suitable for qualitative, non-quantitative sampling (Brenke 2005, Schüller et al. 2009, Chapter 3), which can hamper the comparability to other studies. Even though, the overall composition and the proportion of polychaetes in the macrofauna of the Vema-TRANSIT expedition is largely the same as in other macrofaunal composition studies sampled with an epibenthic sledge (e.g. Linse et al. 2007, Brandt et al. 2014, 2015, Chapter 2).

More detailed considerations of polychaetes in relation to the total macrofauna from the Vema-Transit Expedition (Table 1) reveal slightly lower proportions in the western VFZ (19 %) and a significant decrease in the hadal PRT (9 %). The lower proportion of polychaetes in the western VFZ might be explained with the presence of hard structures like manganese crust and nodules at the sampled sites (Lins et al. 2018a, Devey et al. 2018), as the majority of the collected polychaetes were bottom-dwelling with preference for soft-sediment (Chapter 3). Though, a potential sampling bias caused by the hard structures in the western VFZ should be also taken into account (Chapter 2, 3). The significant low proportion of polychaetes, obtained from the hadal PRT is surprising, as they are supposed to be one of the most abundant and diverse groups of invertebrates in the hadal (Jamieson 2015). The low number of polychaetes (153 specimens, Table 1) found might be caused by disturbances, frequently occurring in the PRT, as well as the low-nutrient, terrigenous clay, which is mainly found this area (Richardson et al. 1995).

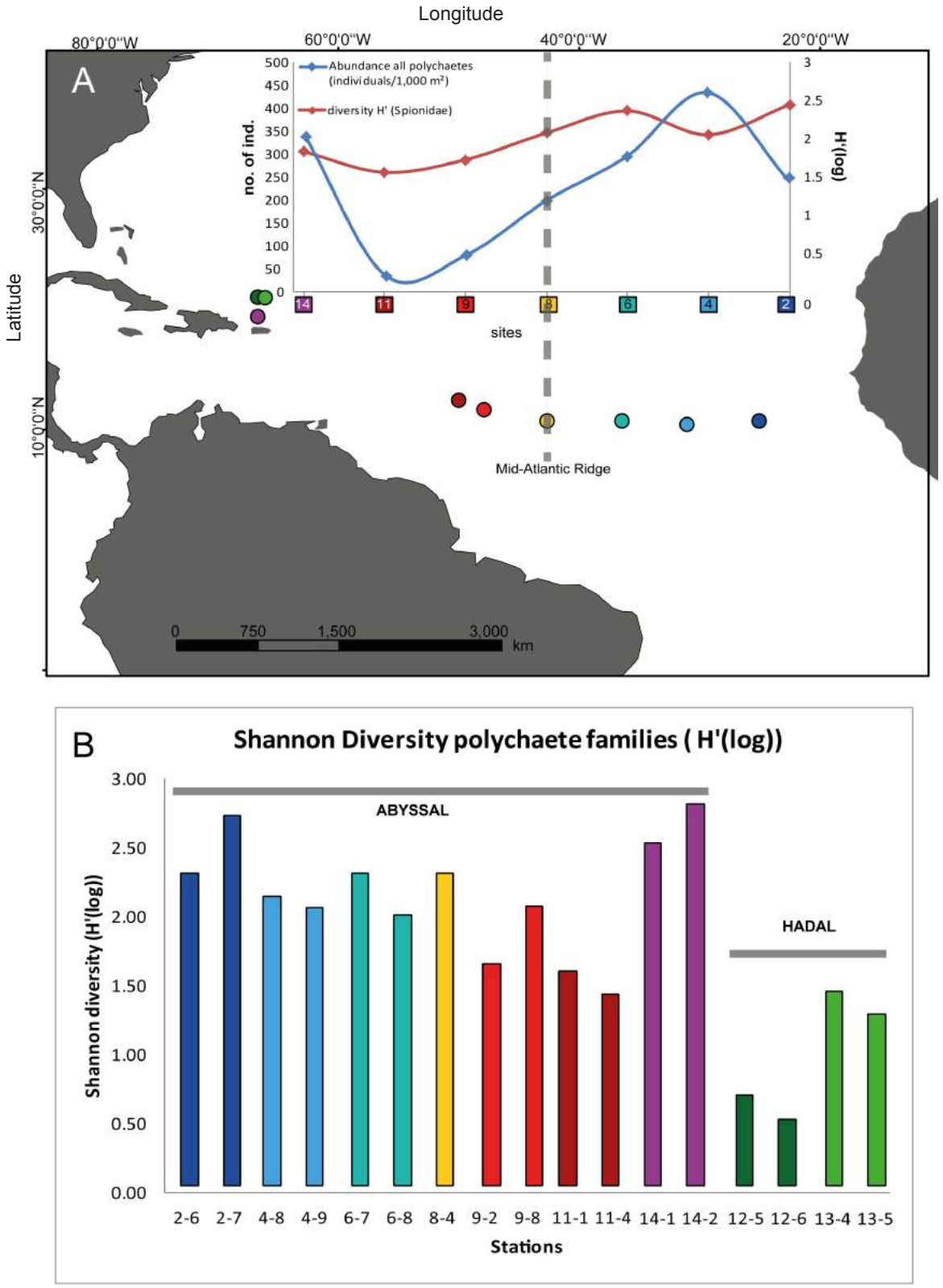

Fig. 1. Diversity (Shannon diversity H') and abundance of polychaetes in the abyssal tropical Atlantic. A. Abundance of all polychaetes and Shannon diversity (H'(log)) of spionids along the sampled sites in the tropical Atlantic. Map is showing sample localities (colour coded) and the position of the Mid-Atlantic Ridge. B. Shannon diversity (H'(log)) of polychaete families from the tropical Atlantic along the sampled stations in the tropical Atlantic. Colours are according to the sampling sites in A.

Regarding the abundances of the polychaetes from the tropical Atlantic, no decline of the abundance with distance from the bathyal continental slopes were observed (see Fig. 1 A; Table 1). The abundance is highest in the middle site of the eastern VFZ and noticeably decreasing towards the western VFZ, followed by a renewed rise in the abyssal PRT (Fig. 1A). But even if the relatively low abundance of polychaetes in the western VFZ is neglected, the parabolic curve in the eastern VFZ suggests that the abundance of the polychaetes in the tropical Atlantic is not depending on the distance to high productive slopes.

Table 1. Absolute numbers of polychaetes in the Vema-Fracture Zone (VFZ), the Vema Transform Fault (VTF) and the Puerto Rico Trench (PRT) in relation to the total macrofaunal invertebrates (modified from Table 2, Chapter 2)

	eastern VFZ	VTF	western VFZ	PRT abyssal	PRT hadal	Total
Total no. of polychaetes	3,518	347	284	725	153	5,027
Total no. of macrofaunal invertebrates	13,552	1,258	1,488	3,333	1,701	21,332
% of polychaetes	26	28	19	22	9	24

An explanation for the observed pattern is that the food flux in this region is proposed to be influenced by a significant input of Sargassum algae from the surface to the abyssal, especially in the eastern VFZ (Baker et al. 2018), which may have a stronger positive influence on the abundance in this area than the distance to land. The occurrence of large floating Sargassum mats is well known, especially from the Atlantic Ocean and the Gulf of Mexico (Gower and King 2008) and also its role as a potential food resource for the deep sea (Wolff 1979, Turner and Rooker 2006).

The overall composition of the polychaete community found in the tropical Atlantic is comparable to other deep-sea areas (Chapter 3) with 41 observed polychaete families, of which Spionidae and Cirratulidae often dominating the assemblages (Cosson-Sarradin et al. 1998, Paterson et al. 1998, Glover et al. 2001, Hilbig and Blake 2006, Fiege et al. 2010).

Next to food flux, habitat heterogeneity in sediment structure is thought to influence species richness and faunistic compositions (e.g. Etter and Grassle 1992, Gray 2002, Leduc et al. 2012, De Smet et al. 2017). Along the VFZ, differences in the sediment composition were observed between the eastern and western abyssal plains. In the eastern VFZ typical deep-sea soft sediment was present, whereas in the western VFZ a higher proportion of coarser sediment, as well as manganese nodules and crust were found (Lins et al. 2018a, Devey et al. 2018, Chapter 2 and 3). These differences probably caused the significant differences in the composition of polychaete families between the eastern and western VFZ,

which are mainly based on the presence and absence of the families Sigalionidae and Pectinariidae (see data analyses Chapter 3). These families were restricted to one of the regions according to their sediment type preferences, with Sigalionidae only present in the soft-sediments of the eastern VFZ and the Pectinariidae occurring only in the western VFZ with coarser sediments (Jumars et al. 2015, Chapter 3).

Despite these differences in family composition, derived from sediment preferences of two families, no significant differences were found for the diversity (measured by Shannon's H') between the eastern and western VFZ, neither at family, nor at species level for selected genera (see data analyses Chapter 3; Fig. 1). Consequently, there seems to be no obvious correlation between the diversity and habitat heterogeneity (higher sediment heterogeneity in the western VFZ) or potentially higher food input towards the continental slopes for the herein studied polychaetes.

In fact, an almost stable relative diversity (Shannon's H') was found for the family Spionidae along the abyssal tropical Atlantic (Fig. 1A). Shannon diversity is taking into account the number of species in relation to the abundance (Washington 1984) and both values are lower in the western VFZ than in the eastern VFZ, but as the rarefaction curve was steeper for western VFZ, it can be suggested that a larger proportion of the diversity was not recovered compared to the eastern VFZ (Chapter 3, Fig. 4). Thus, the Shannon diversity for the spionids along the VFZ is comparable, and with values slightly varying between 1.56 and 2.36 (Fig. 1A), no apparent influence of habitat heterogeneity and distance to productive slopes is observable.

As already mentioned, factors like food input and habitat heterogeneity are observed to have a major influence on the abundances and composition of deep-sea polychaete populations, thus abundances are reported to decrease with depth and distance from the high productive continental slopes (e.g. Cosson-Sarradin et al. 1998, Rex and Etter 2010). Bathymetric gradients of increasing diversity and decreasing abundance in the benthic deep-sea sediments are welldocumented and accepted as a general pattern (e.g. Rex et al. 2005, Rex and Etter 2010), even though it has been repeatedly stressed that such general patterns are often taxon specific, as well as potentially different on spatial scale and hence should be considered with caution (e.g. Ellingsen et al. 2007b, Stuart et al. 2017, Wilson 2017). The studied polychaetes within this thesis do not reveal these general patterns. Therefore, the hypotheses that abundance is decreasing with distance from continental slopes, as well as an increasing diversity with food input and habitat heterogeneity should be questioned, at least for polychaetes in the tropical Atlantic.

For the deepest parts of the oceans, the hadal depths, diversity usually is found to be lower compared to abyssal depths (Fujii et al. 2013, Jamieson 2015). This appears to be also true for polychaetes studied herein, as the diversity is remarkably lower in the hadal (stations 12 and 13) than in the adjacent abyssal (stations 14), as well as in the majority of the abyssal regions along the VFZ (Fig. 1 B). As already mentioned, polychaetes are usually found to be among the most abundant groups in the hadal (Jamieson 2015). Also within the Puerto Rico Trench (PRT) fauna polychaetes were found among the most abundant groups, but the number and proportion of polychaetes were low (Table 1) compared to a surprisingly high abundance of crustaceans (Chapter 2). This might be explained by the sediments within this trench, potentially favouring members of the crustaceans with burrowing lifestyles (Riehl et al. 2018b). The sediments of the hadal depths of the PRT are described to have low-nutrient content and organic carbon-poor silt-clay (Richardson et al. 1995, Levin and Gooday 2003, Devey et al. 2018). The sediment structure, as well as the low food supply might have a major influence on polychaete diversity in the PRT, but further sampling effort is needed to draw conclusions on polychaete diversity in the hadal PRT. At least, it can be concluded that the diversity of polychaetes in the hadal PRT is lower than in the investigated abyssal within the same survey.

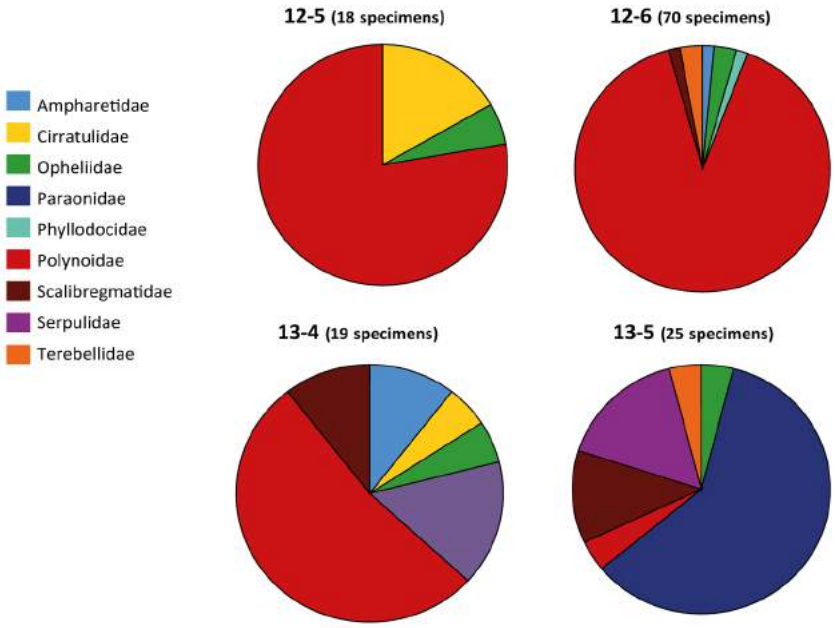

Fig. 2. Polychaete family composition at hadal stations of the Puerto-Rico Trench.

Despite the low abundance of polychaetes found in the PRT, the dominance of polynoids at most of the sampled hadal stations (Fig. 2) was expectable, as high abundances of Polynoida for depths exceeding 6,000 m were previously reported

(Lemche et al. 1976, Beliaev and Brueggeman 1989, Jamieson 2015). The high number of Paraonidae at one station (Fig. 2) is noteworthy, as this family was not recorded before from hadal depths (Jamieson 2015). These findings are again emphasizing the need of further studies on the polychaetes from the hadal PRT.

II. Rare species in the deep sea

When investigating the abundance and diversity in both terrestrial and marine ecological communities, it is often observed that most specimens belong to a few high abundant species and many species are represented by a small number of specimens (e.g. Carney 1997, Magurran and Henderson 2003, Lyons et al. 2005, Kunin and Gaston 2012). In this context the term 'rare' came up and was used in many biological studies in different definitions (reviewed in Kunin and Gaston 2012). The broad consensus of the different usages of the term is that species with low abundance and/or small range sizes are regarded as rare (Ellingsen et al. 2007b, Carney 1997, Kunin and Gaston 2012). Both, range size and abundance are found to be often positively correlated, but dependant on habitat characteristics (Gaston and Lawton 1990), as the number of rare species seem to "…increase with both within-and between-site heterogeneity and that these relationships may arise from habitat-specific species with restricted range size…." (see Ellingsen et al. 2007b: p. 298).

A high number of rare species is also observed in many benthic deep-sea studies consistently, whereas they are mostly defined as species with low abundances (singletons or doubletons) and narrow distribution ranges (e.g. Glover et al. 2001, 2002, Ellingsen et al. 2007b, Fiege et al. 2010). For instance, Ellingsen et al. (2007b) revealed a high proportion of rare polychaetes and isopods in the Atlantic sector of the Southern Ocean, as well as Brandt et al. (2005), which found rarity in 49% of peracarid species in the Angola Basin. Comparable patterns were also observed in the Pacific (Glover et al. 2002) and the Atlantic abyss (Glover et al. 2001, Linse and Schwabe 2018).

Also within the Spionidae (Chapter 4: Laonice; Chapter 5: Prionospio and Aurospio) and the Polynoidae (Chapter 6: Bathypolaria) from the tropical Atlantic that were studied with molecular tools rare species were found (Laonice: ~ 62.5 % of the species; Prionospio/Aurospio: ~ 18.7 % of the species; Bathypolaria: ~ 66.6 % of the species). For these genera studied in detail in my thesis, the classification rare is related to a recognizable low abundance (singletons or doubletons) at the respective studied sites. Some of these rare species show a geographically restricted range, especially in Laonice three out of eight species were found to be rare and occurred at most at two adjacent sites (see Laonice sp. A, sp. B, sp. C, sp. E in Fig. 3 in Chapter 4). Not considering the Prionospio species restricted

to the Pacific, three out of 16 Prionospio species can be categorised as rare, but all of exhibited rather wide distribution ranges (see Prionospio sp. A, sp. I, sp. N in Fig. 3 in Chapter 5). A similar situation can be found for Bathypolaria, although the delineation of lineages in Bathypolaria is not as clear (Chapter 6). Nevertheless, at least two species out of three are found to be rare, but with a potentially wide distribution (see Bathypolaria lineages B and C in Fig. 3 in Chapter 6). These findings are supporting the presence of a high proportion of rare species in the deep sea, which are mainly contributing to differences in diversity at regional scales (Ellingsen et al. 2007b), but the number of specimens contributing to these rare species is comparatively low (Laonice: ~ 10 % of individuals; Prionospio/ Aurospio: ~ 3.3 % of individuals; Bathypolaria: 20.6 % of individuals).

Several rare species were wide-spread, occurring at up to four sites more than 2,500 km apart, or even pan-oceanic (e.g. see Chapter 5, Prionospio sp. A and sp. N). However, the findings contradict the assumption that the low abundance of rare species is correlated with restricted dispersal capabilities (e.g. Gaston and Lawton 1990, Ellingsen et al. 2007a) and rarity may not equate to restricted distribution, which was already also observed for the gastropod Palazzia planorbis (Dall 1927), occurring across the whole Atlantic (Rex 2002).

These species may represent species with wide geographic distributions but low population densities. Such low population densities are suggested to potentially result in limited reproductivity and the ability of populations with such low density to persist is proposed to be results of a source-sink system originating in the immigration of species from the highly productive shallow water (source) to the depauperate deep sea (sink) (Rex et al. 2005, Moreno et al. 2008). Consequently, the intensity of these ‘sinking’ bathyal species would have a direct influence on the viability of abyssal low abundant populations (Rex et al. 2005). Such dependency of abyssal populations on bathyal species should prevent the evolution of unique haplotypes for rare abyssal individuals and the haplotype diversity should decrease with distance to potential bathyal source populations (Rex et al. 2005). An actual source-sink system for rare species in the tropical Atlantic is rather unlikely, as none of the molecular studied polychaetes from this area exhibit such a proposed pattern in their haplotype networks (see Figs. 3 in Chapter 4, 5 and 6). Furthermore, a source-sink dependency of rare species in the abyssal would expect the occurrence of the same species in the bathyal. As only few specimens from bathyal depths were included in the studies (available from GenBank: see Supplements Chapter 4, 5; Table 1 in Chapter 6), the molecularly studied polynoids and spionids from the tropical Atlantic are not sufficient for clearly rejecting or supporting the idea of a source-sink system. Hence, it seems rather unlikely to find the same species in the bathyal, because, as already mentioned, the dis-

tance to the potential bathyal source has no influence on the haplotype diversity in the abyssal and a dispersal of shallow water specimens across several hundreds or thousands of kilometres into the abyssal is doubtful.

Another suggested scenario is that rare species are part of large-scale metapopulations with higher abundances in regions not included in the sampled area (Rex et al. 2005). This scenario might be a possible explanation, but as the studied spionids and polynoids from the tropical Atlantic are sampled along a large east-west transect over 4,600 km and none of the species are indicating such population pattern, at least this seems to hold not true for these polychaetes.

However, the results within this thesis are strongly indicating a wide distribution potential of species despite low abundances, and do not indicate a bathyal source for rare species or limited reproductivity in the abyssal. It remains unclear if the high number of rare species recorded in deep-sea samples (e.g. see Glover et al. 2001, 2002, Ellingsen et al. 2007b, Fiege et al. 2010) are reflecting the real biodiversity or if broader scale sampling would reduce the proportion of rare species by equalling out local differences in abundances.

III. Distribution patterns in the tropical Atlantic

Dispersal abilities of species are certainly a crucial factor influencing spatial diversity, species turnover, persistence of populations and colonization in the deep sea (e.g. McClain et al. 2012, Zakas and Hall 2012, Baco et al. 2016). In accordance with the general assumption of the abyssal to be a continuous, almost homogenous habitat, it is regularly proposed that geographically wide distribution ranges are much more common in the abyssal compared to the bathyal or shallow depths (Bradbury et al. 2008, McClain and Hardy 2010, Yearsley and Sigwart 2011, Higgs and Attrill 2015). Wide distribution ranges, from the Caribbean to the abyssal plain near West-Africa, were indeed found for the abyssal Spionidae (Laonice: Chapter 4; Prionospio and Aurospio: Chapter 5) and Polynoidae (Bathypolaria: Chapter 6) studied from the tropical Atlantic.

Probably an important factor in explaining such wide distribution ranges is dispersal during planktonic larval stages (Young et al. 1997, Schüller and Ebbe 2007, McClain and Hardy 2010, Rex and Etter 2010, Yearsley and Sigwart 2011, Taylor and Roterman 2017). Even though, some benthic invertebrates, like for instance some Holothuroidea are highly mobile (Rogacheva et al. 2012), the majority of deep-sea invertebrate taxa are relatively non-motile as adults (McClain and Hardy 2010). Also the herein studied Spionidae usually live in tubes with limited motility as adults (Jumars et al. 2015). In the Arctic Ocean Bathypolaria species were observed swimming (MacDonald et al. 2010). Also non-mobile adults might

be dispersed by benthic storms and currents as these are able to transport large amounts of sediment (Scheltema 1994, Stow et al. 2002) and of the associated benthic fauna (Schüller and Ebbe 2007). However, such events alone are very unlikely to have caused such widespread distribution patterns. Our knowledge about larval and developmental modes of deep-sea invertebrates is still sparse and for many taxa and species the larvae and their mode of development are unknown (e.g. Young 2003). But both, Spionidae and Polynoidae, usually have planktonic larval stages (Glasby et al. 2000, Blake et al. 2018) and the herein observed wide dispersal capacities are a strong indication for distribution of the studied species via planktonic larvae (Scheltema 1972). Large geographical distribution ranges are not solely based on the presence of planktonic larval stages and the subsequently dispersal potential (e.g. Paulay and Meyer 2006, Lester et al. 2007, Shanks 2009, Hilário et al. 2015). It is rather a species-specific combination of different intrinsic and extrinsic factors influencing distribution boundaries, like the speed of currents transporting the larvae, larval behaviour, as well as settlement probability according to changes in temperature, oxygen and hydrostatic pressure (e.g. Young et al. 1997, Paulay and Meyer 2006, Fiksen et al. 2007, Pineda et al. 2009, Yearsley and Sigwart 2011, Hilário et al. 2015). Another important factor influencing distribution ranges is the successful settlement of larvae in a habitat, whereby larval settlement is responding to different chemical, sedimentological and abiotic factors (e.g. Eckman 1996, Kingsford et al. 2002, Metaxas and Saunders 2009). Topographic features like seamounts or mid-oceanic ridges can disrupt the currents, which are transporting planktonic larvae, hence limiting dispersal ranges (Stow et al. 2002, McClain and Hardy 2010).

The MAR is one of the most important topographic features in the Atlantic, dividing it in two oceanic basins and having a striking influence on the circulation of bottom water (Mauritzen 2002, Levin and Gooday 2003). As the VFZ is interrupting the MAR, it allows the exchange of deep and intermediate water masses between the ocean basins (Eittreim and Ewing 1975, Stow et al. 2002). Consequently, it seems reasonable that the VFZ is also a passage for the deep-sea fauna to disperse between the eastern and western parts of the abyssal Atlantic. There are strong indications that the polychaetes investigated from the tropical Atlantic are able to disperse through the VFZ. Many of the Laonice (Chapter 4: Laonice sp. D, sp. H), Prionospio and Aurospio (Chapter 5: Prionospio sp. B, sp. D, sp. G, sp. L, sp. M, sp. O; Aurospio cf. dibranchiata) species, as well as the Bathypolaria lineages (Chapter 6: Bathypolaria lineages A, B) showed no restriction to either side of the MAR. They rather showed ongoing gene flow between the eastern and western VFZ as shared haplotypes or only very little genetic differentiation between the populations was observed (see Figs. 3 in Chapter 4, 5 and 6). Taking into account that many of these trans-MAR occurring species

are also found in the Vema Transform Fault, the hypothesis of the VFZ to be a connection through this potential topographic barrier is very likely (see iscussion Chapter 3, 4, 5 and 6).

The results do not allow to infer the direction of gene flow, hence it remains unknown, if dispersal occurs via passive transport with the strong eastwards currents of the Antarctic Bottom Water (AABW) or the slower westwards overflowing North Atlantic Deep-Water (NADW) (Fischer et al. 1996, Mauritzen 2002, Devey et al. 2018) or both.

Distribution ranges across the MAR, most likely through the VFZ was also observed for other taxa with planktonic larvae like macrofaunal molluscs (Linse and Schwabe 2018), but also for direct developing Nematoda (Lins et al. 2018b). The VFZ as a passage, enhancing distribution of benthic deep-sea macrofauna seems to be limited to species with enhanced dispersal capabilities. The majority of the predominantly benthic Peracarida investigated from the same sampling sites and the same gear in the tropical Atlantic showed a restricted distribution to either the eastern or western side of the MAR (e.g. Riehl et al. 2018b, Bober et al. 2018, Brix et al. 2018). It was suggested that trans-MAR distributed species are more effective in dispersion according to their mobility, like the Atlantic-wide distributed Acanthocope galathea Wolff, 1962, which is proposed to be a good swimmer (Bober 2018b).

The Peracarida are brooders without larval stages, and their often observed restricted distribution is supporting the postulated theory that taxa with larval dispersal have generally wider distribution ranges than brooders (e.g. Baco et al. 2016). But it has to be recognized that high dispersal potential of planktonic larvae are not direct correlating with distribution ranges (e.g. Paulay and Meyer 2006, Shanks 2009, Hilário et al. 2015). As already mentioned, it is rather an interaction of intrinsic and extrinsic factors influencing distribution ranges of benthic invertebrates (Metaxas and Saunders 2009, McClain and Hardy 2010, Yearsley and Sigwart 2011). These different factors influencing dispersal potential might explain the differences, which can be observed when comparing the distribution patterns in the tropical Atlantic between the investigated polychaete genera (Chapters 4, 5 and 6). For the investigated spionid genera from the tropical Atlantic about half of the Prionospio and Aurospio species were found to be distributed across the MAR (Chapter 5), which is twice as much as the one fourth observed trans-MAR species for Laonice (Chapter 4). Even though, two third of the lineages found for the polynoid Bathypolaria were occurring on both sides of the MAR, one of them (lineage B, Chapter 6) shows much more genetic differentiation between the individuals on the different sides than found for both spionid genera. In consideration of all results obtained for the distribution patterns in the tropical Atlantic (Chapter

4, 5, 6), Prionospio and Aurospio seem to have a generally higher horizontal dispersal potential than Laonice and Bathypolaria. One explanation could be a much more opportunistic and successful adaption to different environmental conditions of these genera, as the eastern and western VFZ differs in sediment composition, temperature and salinity (Devey et al. 2018). Next to effects of abiotic factors on successful settlement, there are other processes influencing the recruitment of specimens. The post-settlement survival to adulthood is crucial for the viability of a population in a specific environment and incorporates predators, inter-specific and intra-specific competition for space and food, as well as habitat suitability and disturbances (e.g. Wilson 1990, Fraschetti et al. 2002, Pineda et al. 2009)

It has been reported that some Spionidae are highly successful in adaption to changing food flux as they have the ability to switch their feeding type from suspension to deposit feeding in accordance with available food supply (Dauer et al. 1981, Nowell et al. 1984, Jumars et al. 2015, Blake et al. 2018). Even though, these switching of feeding modes of spionids are almost solely based on observations in shallow water species, it appears to be logical that deep-sea species have the same competences, regarding the benefits to switch between feeding in the water column and sediment surface and the resulting ability to utilize a wide variety of food resources (Dauer et al. 1981). Furthermore, an unusual mode of active, palp-waving suspension feeding observed for an unidentified deep-water Prionospio species (see citation Popovich et al. 2015 in Jumars et al. 2015) may indicate a general potential of this genus for special feeding adaptions in deep-sea environments.

Another explanation for the differing distribution ranges could be the overall higher number of individuals, especially found for Prionospio, as positive correlations between the numbers of propagules produced and dispersal abilities was proposed (Pineda et al. 2009). However, such a relation has to be treated with caution, as nothing is known about how and in which intensity the investigated species reproduce

Nonetheless, in summary a high number of the in detail investigated polychaetes (Chapters 4, 5 and 6) showed high dispersal potential over large geographic distances and across the MAR in the tropical Atlantic, which agree with the assumption that deep-sea polychaetes tend to be widespread (e.g. Schüller and Ebbe 2007, Paterson et al. 2009, Wilson 2017).

Next to horizontal distribution patterns of the polychaetes in the tropical Atlantic, vertical distribution ranges and a potential depth related barrier between the abyssal Atlantic and the hadal PRT could be studied. Spionidae were absent in the hadal depths, but polynoids (mainly Bathypolaria) were found in high abun-

dances (Fig. 2). The analyses of Bathypolaria additionally revealed an enormous vertical distribution range (> 4,000 m) for one of the lineages, with identical haplotypes occurring in the hadal depths of the PRT as well as the eastern most site close to West-Africa (lineage A; Chapter 6). Polynoidae are commonly found in hadal depths, sometimes in high abundances (Lemche et al. 1976), but most of them are classified as restricted to depths over 6,000 m (Beliaev and Bruggeman 1989). Hence, such a wide vertical distribution range was not expected, as an often observed general pattern is that depth is influencing distribution ranges much more than horizontal distances (e.g. Zardus et al. 2006, McClain and Hardy 2010, Schüller 2011, Taylor and Roterman 2017). This depth-dependent pattern of distribution is mainly based on differences between bathyal and abyssal depths and Paterson et al. (2009) already found a remarkable number of polychaetes with wide bathymetric ranges recorded from abyssal and hadal depths, but to my knowledge, the data presented in Chapter 6 is the first molecular proof for a hadal-abyssal distributed polychaete with recent gene flow.

Species in the deep sea with large eurybathic distribution are generally proposed to result from source-sink systems (see section II), which is supported by the findings that many abyssal species with large bathymetric ranges are also found in shallower depths, where productivity, abundance and biomass is usually found to be remarkably higher than in the deep-sea (Rex et al. 2005, Moreno et al. 2008). As already mentioned, the diversity in the hadal zone is supposed to be lower than in the abyssal (see section I). Accordingly to this decrease of diversity with increasing depth, i.e. a bathymetric gradient of species richness was proposed that a source-sink system may is also applicable to the hadal, with species deriving in the hadal from populations inhabiting abyssal or even bathyal depths (Paterson et al. 2009).

Like the already mentioned discrepancy of the presented results in this thesis and a potential source-sink system in rare species (see section II), the results from the studied Bathypolaria lineages are supporting a different scenario. The majority of the specimens were obtained from the hadal PRT (~ 74 %) and only few individuals were found in the abyssal depths of the tropical Atlantic (~ 26 %), with none occurring in the abyssal surrounding the trench (Table 1 in Chapter 6). The higher genetic diversity that was found in the hadal specimens of lineage A in the slow evolving nuclear 18S gene, indicate a more ancient population in the hadal compared to the abyssal (Discussion in Chapter 6). Thus, contrary to the common source-sink system in which evolutionary novelties are supposed to appear in shallow-water zones, dispersed towards the deeper zones (Moreno et al. 2008), a colonisation of the abyssal from the hadal should be considered, at least for this species. It was already mentioned that a temporary bidirectional dispersal

between source and sink is possible, but it was linked to an increase in food input (Gonzalez and Holt 2002, Rex et al. 2005), which was not observed in the PRT. Consequently, future studies should not exclude the potential of the hadal to be the 'source' and the shallower depths to be the 'sink'.

In any case, Bathypolaria species seem to have significant adaption abilities, either as adults or the larvae, to various environmental variables including hydrostatic pressure, temperature and sediment composition. Both, changing pressure and temperature can have strong influence on the colonisation potential of species (Young et al. 1994, Tyler and Young 1998, MacDonald et al. 2010). The large vertical distribution range of Bathypolaria is another example of the high dispersal potential of deep-sea polychaetes. Especially, as such pattern was so far not observed for other benthic macrofaunal taxa sampled in the same survey, neither for isopods, which are known to be poor dispersers (Riehl et al. 2018b), nor for planktonic larval stages bearing molluscs (Linse and Schwabe 2018).

Further studies on polychaetes in hadal trenches, carefully compared to abyssal or even bathyal recorded species would help to reveal if source-sink colonization events with the deeper zones as the source might be more common than previous assumed.

IV. Pan-oceanic distribution patterns

Historically, cosmopolitan distribution (see Introduction Section III) was already proposed to be very common for polychaetes in the mid-19th century (e.g. Grube 1850, Quatrefages 1865). A high degree of intraspecific variations (Fauvel 1959) and a wide geographic distribution was thought to distinguish polychaetes from other invertebrates in the frequency of cosmopolitism species (e.g. Ekman 1953, Day 1967, Briggs 1974). This assumption is probably a result from the history of polychaete research, as key polychaete taxonomists like Pierre Fauvel (e.g. 1917, 1922, 1923, 1927), John Day (1967) and Olga Hartman (1959, 1965) were supporters of a cosmopolitan polychaete species concept, though they synonymised many species without explanations when they intensively studied polychaetes collected worldwide (Hutchings and Kupriyanova 2018). The view on this cosmopolitan polychaete species concepts started to change in the late 20th century, when first revisions on cosmopolitan polychaetes were arising (e.g. Fauchald 1984, Williams 1984, Hutchings and Glasby 1991). At present, it is thought that cosmopolitism in polychaetes is rather the exception for shallow water species, but occurs more frequently in deep-sea polychaetes (Hutchings and Kupriyanova 2018), which is proposed to be linked to the higher stability and homogeneity of the deep-sea compared to the more heterogeneous shallow depths (e.g. McClain and Hardy 2010)

The widespread distribution potential across large geographic scales in the tropical Atlantic was shown for some polychaetes in the course of this thesis (see previous section). All molecular studies (Chapter 4, 5 and 6) included all sequences for species of the same genera available from GenBank, respectively. Additionally, it was possible to further include a large amount of so far unpublished Prionspio and Aurospio specimens from the Clarion-Clipperton Fracture Zone in the central Pacific to get a comprehensive overview on distribution ranges of these two spionid genera (Chapter 5).

In total, five Prionospio and two Aurospio species (Prionospio sp. A, B, E, H, N and Aurospio cf. dibranchiata, sp. S) were found to have a pan-oceanic distribution with identical haplotypes or haplotypes separated by only few mutational steps between the Atlantic and the Pacific. Despite significant differences between populations from the different oceans, recent gene flow with low rates insufficient for population admixture was concluded (Chapter 5). A potential pan-oceanic distribution was also found to be possible for Bathypolaria, although an apparent differentiation between specimens from the Atlantic and Pacific was revealed and species delimitation was not unequivocal (Chapter 6). Only for Laonice, none of the specimens analysed from the tropical Atlantic were found to be conspecific with Laonice species from other localities, neither from the Atlantic, nor any other Ocean, keeping in mind that comparable data was sparse for the genus (Chapter 4).

Prionospio and Aurospio species seem to have a general higher ability for pan-oceanic or cosmopolitan distribution. A potential for cosmopolitan or at least widespread distribution of Aurospio and Prionospio in the deep sea was already suggested and reported before, like a cosmopolitan distribution of Aurospio dibranchiata Maciolek 1981 (Mincks et al. 2009, Paterson et al. 2016). Also, the observed smaller distribution ranges of Laonice (compared to Aurospio and Prionospio) is in congruence with recent studies on this genus, which revealed genetically different subclades according to their geographic location of the former cosmopolitan reported Laonice cirrata (Sars, 1851) (Bogantes et al. 2018). The distribution capacities of these three spionids (Laonice, Prionospio and Aurospio) are putatively rather linked to specific differences in their life histories and biological response to different environmental conditions, than lacking connectivity for dispersal. Thus, generalising distribution patterns for families and even genera has to be treated with caution. Bathypolaria species also show a potential for large horizontal distribution ranges, maybe even across oceans, but they seem to be more specialized on vertical distribution (Chapter 6).

These different patterns are supporting the assumption that predictions about general distribution patterns for polychaetes seems to be difficult at the moment,

as they are rather species-specific and factors mainly influencing these patterns are often unknown for deep-sea taxa. Nonetheless, with intensive studies at a global scale, we might get a better perspective on the distribution ranges of species and the importance of conservation of deep-sea habitats for the viability of global populations. Furthermore, the obtained results within this thesis are strongly supporting the hypotheses that cosmopolitan or at least pan-oceanic distributions occur in deep-sea polychaetes, but are an exception and not the rule.

V. Importance of differentiation of polychaete species

There is an essential importance of species identification and differentiation when studying diversity and distribution patterns of deep-sea polychaetes (e.g. Glover et al. 2015, 2018). Due to sparse taxonomic knowledge about deep-sea polychaetes, missing species-specific characters caused by damaging or fragmentation during sampling processes and often reported cryptic species, the morphological identification is often extremely challenging (see Introduction, section V; discussions Chapter 3, 4, 5 and 6). The use of molecular analyses showed partially high discrepancies between the morphologically identified polychaetes (Chapter 3) and genetically delineated species (Chapter 4, 5, 6). Indeed, the assignment to the respective families and genera were consistent with molecular results, but at species level the results were rather different. For instance, the morphological identification of Aurospio and in particular Prionospio species (Chapter 3) was not supported by the molecular species delineation (Chapter 5). Both spionid genera are rather fragile and as important characters were often missing in the studied specimens, morphological identification success was limited. Furthermore, the difficulties with their taxonomy may not be surprising, as both are assigned to the so called Prionospio-complex, in which generic characters are overlapping and still under debate (e.g. Paterson et al. 2016, Chapter 5). Differences between morphological and molecular studies on Laonice were less pronounced (Chapter 3). Even though also all specimens were incomplete, fewer damages in combination with available intensive studies on the taxonomy of deep-sea Laonice (e.g. Sikorski 2003, Sikorski and Pavlova 2016, Sikorski et al. 2017) could be one factor explaining it. Furthermore, Laonice are typically more robust and have a larger body compared to Prionospio species (Blake et al. 2018). The differences between morphology and molecular analyses observed for Laonice species were proposed to derive mainly from misinterpretation of interspecific differences as intraspecific variations (Chapter 4). The delimitation of species for the hitherto monotypic genus Bathypolaria also showed strong inconsistencies between morphology and genetics, which was again interpreted as mainly derived from damages during sampling procedure and fixation (Chapter 6).

The differences between morphological and molecular species delimitation resulted in different results on diversity and distribution of the polynoid and spionids studied in detail. In general, there was a slightly higher or comparable number of species found with molecular tools (see discussions Chapter 4, 5 and 6) and a trans-MAR distribution is found with both methods. However, there was a potential overestimation of the number of specimens belonging to the most dominant species, when identified with morphology. This was mainly observed in Prionospio, Aurospio and Laonice. All three genera were reported to comprise one highly abundant species, if identification was based solely on morphology (Chapter 3: Aurospio cf. dibranchiata, Laonice cf. blakei and Prionospio sp. 8), which were split each into different species with a molecular approach.

These findings are highlighting the limits of solely morphological studies with deep-sea polychaetes at species level. Even though the use of molecular data helped to solve some morphological misinterpretations, molecular tools are also limited. For instance, the molecular studies were mainly based on mitochondrial marker (COI and 16S), which are known to bear some sources of error as well, like the retention of ancestral polymorphism, male-biased gene flow, hybrid regression and paralogy (Moritz and Cicero 2004, Galtier et al. 2009). In the different studies (4, 5 and 6), the additional analyses of a nuclear gene (18S) was used to improve the results of the mitochondrial genes, but still a margin for interpretation for species boundaries is left. This was mainly observed in the analyses of Bathypolaria specimens, which could not be unambiguously delimited into multiple species (Chapter 6).

One improvement for these issues could be the use of next-generation sequencing approaches to obtain information from whole or large portions of the specimens' genomes (e.g. Fonseca et al. 2010, Willette et al. 2014). Despite the benefits of next-generation sequencing, abyssal biodiversity and biogeography studies should be performed using a systematic evolutionary approach including both, molecular and morphological investigations (Glaubrecht 2007, 2010, Schwentner et al. 2014).

VI. Conclusion

The studies presented in this thesis are contributing towards a better understanding of diversity and distribution patterns of polychaetes in the deep sea. Interestingly, some general hypotheses on deep-sea diversity seem to be not applicable for polychaetes in the tropical Atlantic.

A decreasing abundance with distance from the highly productive continental slopes, as well as an increasing diversity with habitat heterogeneity and increas-

ing food input was not observable. A potential correlation with the large floating Sargassum mats as food source in the studied area may be one of the factors contributing to theses differing patterns, but there is rather a complex interaction of many more factors, which are worth to be identified.

Furthermore, a wide distribution range was found for both, rare and high abundant species, emphasizing the incomplete definition of what rare species really are, their origin and their impact on deep-sea biodiversity. The presented studies are revealing an overall wide distribution potential of some polychaetes in the deep sea. The ability to distribution across the MAR in the tropical Atlantic was shown for all studied genera, with the VFZ playing most likely a major role in the dispersal. As a potential pathway for benthic abyssal fauna was doubted recently for the majority of species (Bober 2018b), additional sampling close to other Fracture Zones, as well as from abyssal locations near the MAR without disruptions would help to elucidate the potential barrier effect of this topographic feature.

The enormous dispersal potential of some species was further demonstrated with pan-oceanic distribution ranges, also confirming the existence of cosmopolitism in deep-sea polychaetes. Understanding the way of dispersal over such large geographic distances, could be improved by more comprehensive samples, preferably in comparable depths along deep water masses connecting the different ocean basins like the AABW. Identifying populations potentially acting as “stepping stones” between areas far apart, could promote studies on distribution patterns and population structures in the deep sea.

Hypothesis on lower diversity in hadal depths could be confirmed with the herein studied polychaetes, but a surprising distribution pattern was found for at least one species. One lineage of Bathypolaria was found to have a large bathymetric range (> 4,000 km). The molecular analyses are indicating a potentially origin in the hadal, which is remarkable and oppositely to a general assumption that hadal species are resulting from sinking populations in shallower depths. It remains unclear, if Bathypolaria is an unusual case or if it is occurring more frequently in other species. Further comparison of hadal and abyssal polychaetes would be certainly help to reveal such patterns.

The studies presented in this thesis are showing that diversity and distribution patterns are taxon-specific and illustrating that general pattern should be formulated carefully, as many species-specific factors may influence such patterns. Further studies with the other polychaete families from the tropical Atlantic at species level, especially those having other lifestyles and dispersal strategies than the studied spionids and polynoids would be definitely useful and interesting for comparison.

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Eidesstattliche Versicherung Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Affirmation in lieu of oath I hereby declare, on oath, that I have written the present dissertation on my own and have not used other than the acknowledged aids.

Signature / Unterschrift

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To whom it may concern!

21.06.2019

Dissertation und Publikationen von Theresa Margarete Guggolz

Sehr geehrte Damen und Herren,

hiermit bestätige ich, dass Frau Theresa Margarete Guggolz in ihrer Dissertationsschrift die Beteiligung der Autoren an den einzelnen Veröffentlichungen darlegt. Ich bestätige ferner, dass ihre Beteiligung der tatsächlichen Arbeitsverteilung entspricht.

Mit freundlichen Grüßen,

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References

Allen, J.A. 2008. Bivalvia Of The Deep Atlantic. Malacologia 50: 57–173.

Baco, A.R.; Etter, R.J.; Ribeiro, P.A.; von der Heyden, S.; Beerli, P.; Kinlan, B.P. 2016. A synthesis of genetic connectivity in deep-sea fauna and implications for marine reserve design. Molecular Ecology 25: 3276–3298.

Baker, P.; Minzlaff, U.; Schoenle, A.; Schwabe, E.; Hohlfeld, M.; Jeuck, A.; et al. 2018. Potential contribution of surface-dwelling Sargassum algae to deep-sea ecosystems in the southern North Atlantic. Deep Sea Research Part II: Topical Studies in Oceanography 148: 21–34.

Ball, M.M.; Harrison, C.G.A. 1970. Crustal Plates in the Central Atlantic. Science 167: 1128–1129.

Ballard, R.D.; Hively, W. 2002. The Eternal Darkness: A Personal History of Deep-Sea Exploration. New Ed ed. Princeton Univ Pr, Princeton, NJ, 408p.

Beliaev, G.M.; Brueggeman, P.L. 1989. Deep Sea Ocean Trenches and their Fauna. .

Bickford, D.; Lohman, D.J.; Sodhi, N.S.; Ng, P.K.L.; Meier, R.; Winker, K.; et al. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology & Evolution 22: 148–155.

Blake, J.A.; Maciolek, N.J.; Meißner, K. 2018. Handbook of Zoology: Spionidae Grube, 1850. In: A Natural History of the Phyla of the Animal Kingdom, Annelida: Polychaeta, Berlin, Boston, p.109 pp.

Bleidorn, C.; Vogt, L.; Bartolomaeus, T. 2003. New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. Molecular Phylogenetics and Evolution 29: 279–288.

Bober, S. 2018b. Abyssal barriers -Phylogeography, distribution and natural history of Asellota (Crustacea) in the deep sea. Universität Hamburg, Hamburg, 234p.

Bober, S.; Brix, S.; Riehl, T.; Schwentner, M.; Brandt, A. 2018. Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean? Deep Sea Research Part II: Topical Studies in Oceanography 148: 91–104.

Bogantes, V.E.; Halanych, K.M.; Meißner, K. 2018. Diversity and phylogenetic relationships of North Atlantic Laonice Malmgren, 1867 (Spionidae, Annelida) including the description of a novel species. Marine Biodiversity 48: 737–749.

Bonifácio, P.; Menot, L. 2019. New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida). Zoological Journal of the Linnean Society 185: 555–635.

Bower, A.S.; Cann, B.L.; Rossby, T.; Zenk, W.; Gould, J.; Speer, K.; et al. 2002. Directly measured mid-depth circulation in the northeastern North Atlantic Ocean. Nature 419: 603.

Bradbury, I.R.; Laurel, B.; Snelgrove, P.V.R.; Bentzen, P.; Campana, S.E. 2008. Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. Proceedings of the Royal Society B: Biological Sciences 275: 1803–1809.

Brandt, A.; Brenke, N.; Andres, H.-G.; Brix, S.; Guerrero-Kommritz, J.; Mühlenhardt-Siegel, U.; et al. 2005. Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. Organisms Diversity & Evolution 5: 105–112.

Brandt, A.; De Broyer, C.; De Mesel, I.; Ellingsen, K.E.; Gooday, A.J.; Hilbig, B.; et al. 2007. The biodiversity of the deep Southern Ocean benthos. Philosophical Transactions of the Royal Society B: Biological Sciences 362: 39–66.

Brandt, A.; Havermans, C.; Janussen, D.; Jörger, K.M.; Meyer-Löbbecke, A.; Schnurr, S.; et al. 2014. Composition and abundance of epibenthic-sledge catches in the South Polar Front of the Atlantic. Deep Sea Research Part II: Topical Studies in Oceanography 108: 69–75.

Brandt, A.; Elsner, N.O.; Malyutina, M.V.; Brenke, N.; Golovan, O.A.; Lavrenteva, A.V.; et al. 2015. Abyssal macrofauna of the Kuril–Kamchatka Trench area (Northwest Pacific) collected by means of a camera–epibenthic sledge. Deep Sea Research Part II: Topical Studies in Oceanography 111: 175–187.

Brasier, M.J.; Harle, J.; Wiklund, H.; Jeffreys, R.M.; Linse, K.; Ruhl, H.A.; et al. 2017. Distributional Patterns of Polychaetes Across the West Antarctic Based on DNA Barcoding and Particle Tracking Analyses. Frontiers in Marine Science 4.

Brenke, N. 2005. An Epibenthic Sledge for Operations on Marine Soft Bottom and Bedrock. Marine Technology Society Journal 39: 10–21.

Briggs, J.C. 1974. Marine Zoogeography. MacGraw-Hill, New York, .

Brix, S.; Bober, S.; Tschesche, C.; Kihara, T.-C.; Driskell, A.; Jennings, R.M. 2018. Molecular species delimitation and its implications for species descriptions using desmosomatid and nannoniscid isopods from the VEMA fracture zone as example taxa. Deep Sea Research Part II: Topical Studies in Oceanography 148: 180–207.

Buesseler, K.O.; Lamborg, C.H.; Boyd, P.W.; Lam, P.J.; Trull, T.W.; Bidigare, R.R.; et al. 2007. Revisiting Carbon Flux Through the Ocean's Twilight Zone. Science 316: 567–570.

Byers, J.; Pringle, J. 2006. Going against the flow: retention, range limits and invasions in advective environments. Marine Ecology Progress Series 313: 27–41.

Carney, R.S. 1997. Basing conservation policies for the deep-sea floor on current-diversity concepts: a consideration of rarity. Biodiversity & Conservation 6: 1463–1485.

Clément, L.; Thurnherr, A.M.; St. Laurent, L.C. 2017. Turbulent Mixing in a Deep Fracture Zone on the Mid-Atlantic Ridge. Journal of Physical Oceanography 47: 1873–1896.

Cosson-Sarradin, N.; Sibuet, M.; Paterson, G.; Vangriesheim, A. 1998. Polychaete diversity at tropical Atlantic deep-sea sites:environmental effects. Marine Ecology Progress Series 165: 173–185.

Costello, M.J.; Chaudhary, C. 2017. Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation. Current Biology 27: R511–R527.

Dall, W.H. 1927. Small shells from dredgings off the southeast coast of the United States by the United States Fisheries steamer Albatross in 1885 and 1886. .

Danovaro, R.; Della Croce, N.; Dell'Anno, A.; Pusceddu, A. 2003. A depocenter of organic matter at 7800m depth in the SE Pacific Ocean. Deep Sea Research Part I: Oceanographic Research Papers 50: 1411–1420.

Danovaro, R.; Corinaldesi, C.; Dell'Anno, A.; Snelgrove, P.V.R. 2017. The deep-sea under global change. Current Biology 27: R461–R465.

Danovaro, R.; Canals, M.; Gambi, C.; Heussner, S.; Lampadariou, N.; Vanreusel, A. 2009. Exploring Benthic Biodiversity Patterns and Hotspots on European Margin

Slopes. Oceanography 22: 16–25.

Dauer, D.M.; Maybury, C.A.; Ewing, R.M. 1981. Feeding behavior and general ecology of several spionid polychaetes from the chesapeake bay. Journal of Experimental Marine Biology and Ecology 54: 21–38.

Day, J.H. 1967. A monograph on the Polychaeta of southern Africa. Museum of Natural History Publications 656: 459–878.

De Smet, B.; Pape, E.; Riehl, T.; Bonifácio, P.; Colson, L.; Vanreusel, A. 2017. The Community Structure of Deep-Sea Macrofauna Associated with Polymetallic Nodules in the Eastern Part of the Clarion-Clipperton Fracture Zone. Frontiers in Marine Science 4.

Devey, C.W. 2015. RV SONNE Fahrtbericht / Cruise Report SO237 Vema-TRANSIT : bathymetry of the Vema-Fracture-Zone and Puerto Rico TRench and Abyssal AtlaNtic BiodiverSITy Study, Las Palmas (Spain) - Santo Domingo (Dom. Rep.) 14.12.14 - 26.01.15. GEOMAR Report, N. Ser. 023 . GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany, 130 pp. (http://oceanrep.geomar.de/28317/). Accessed on 08 Jun. 2019.

Devey, C.W.; Augustin, N.; Brandt, A.; Brenke, N.; Köhler, J.; Lins, L.; et al. 2018. Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench. Deep Sea Research Part II: Topical Studies in Oceanography 148: 7–20.

Díaz-Castañeda, V.; Reish, D.J. 2009. Polychaetes in Environmental Studies. In: Annelids in Modern Biology, John Wiley & Sons, Ltd, p.203–227.

Ebbe, B.; Billett, D.S.M.; Brandt, A.; Ellingsen, K.; Glover, A.; Keller, S.; et al. 2010. Diversity of Abyssal Marine Life. In: McIntyre, A.D. (Ed.), Life in the World's Oceans, Wiley-Blackwell, Oxford, UK, p.139–160.

Eckman, J.E. 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. Journal of Experimental Marine Biology and Ecology 200: 207–237.

Eittreim, S.; Ewing, J. 1975. Verna fracture zone transform fault. : 4.

Ekman, S. 1953. Zoogeography of the sea. 9th ed. Sidgwick and Jackson, .

Ellingsen, K.E.; Hewitt, J.E.; Thrush, S.F. 2007a. Rare species, habitat diversity and functional redundancy in marine benthos. Journal of Sea Research 58: 291–301.

Ellingsen, K.E.; Brandt, A.; Ebbe, B.; Linse, K. 2007b. Diversity and species distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. Polar Biology 30: 1265–1273.

Etter, R.J.; Grassle, J.F. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360: 576.

Etter, R.J.; Boyle, E.E.; Glazier, A.; Jennings, R.M.; Dutra, E.; Chase, M.R. 2011. Phylogeography of a pan-Atlantic abyssal protobranch bivalve: implications for evolution in the Deep Atlantic. Molecular Ecology 20: 829–843.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. .

Fauchald, K. 1984. Polychaete distribution patterns, or: can animals with Palaeozoic cousins show large-scale geographical patterns? Proceedings of the First International Polychaete Conference: 1–6.

Fauchald, K.; Rouse, G. 1997. Polychaete systematics: Past and present. Zoologica Scripta 26: 71–138.

Fauchald, K. (Univ of S.C.; Jumars, P.A. 1979. Diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol.; (United States) 17.

Fauvel, P. 1917. Annélides polychètes de l'Australie méridionale. Archives de Zoologie Experimentale et Generale 56: 159–278.

Fauvel, P. 1922. Annélides polychètes de l'Archipel Houtman Abrolhos (Australie occidentale) recueillies par M. le Prof. W. J. Dakin, F.L.S. Journal of the Linnean Society of London 34: 487–500.

Fauvel, P. 1923. Un nouveau serpulien d'eau saumâtre Mercierella n. g., enigmatica n. sp. Bulletin de la Société Zoologique de France 47: 424–430.

Fauvel, P. 1927. Polychètes sédentaires. Addenda aux errantes, Arachiannélides, Myzostomaires. In: Faune de France. Vol. 16. Librairie de la Faculte des Sciences Paul Lechevalier, Paris, .

Fauvel, P. 1959. Classes des annélides polychètes. Distribution géographique. Traité de Zoologie 5: 163–165.

Fiege, D.; Ramey, P.A.; Ebbe, B. 2010. Diversity and distributional patterns of Polychaeta in the deep South Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 57: 1329–1344.

Fiksen, ø; Jørgensen, C.; Kristiansen, T.; Vikebø, F.; Huse, G. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Marine Ecology Progress Series 347: 195–205.

Fischer, J.; Rhein, M.; Schott, F.; Stramma, L. 1996. Deep water masses and transports in the Vema Fracture Zone. Deep Sea Research Part I: Oceanographic Research Papers 43: 1067–1074.

Fonseca, V.G.; Carvalho, G.R.; Sung, W.; Johnson, H.F.; Power, D.M.; Neill, S.P.; et al. 2010. Second-generation environmental sequencing unmasks marine metazoan biodiversity. Nature Communications 1.

Fraschetti, S.; Giangrande, A.; Terlizzi, A.; Boero, F. 2002. Pre- and post-settlement events in benthic community dynamics. Oceanologica Acta 25: 285–295.

Fujii, T.; Kilgallen, N.M.; Rowden, A.A.; Jamieson, A.J. 2013. Deep-sea amphipod community structure across abyssal to hadal depths in the Peru-Chile and Kermadec trenches. Marine Ecology Progress Series 492: 125–138.

Gage, J.D.; Tyler, P.A. 1992. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, 532p.

Galtier, N.; Nabholz, B.; GléMin, S.; Hurst, G.D.D. 2009. Mitochondrial DNA as a marker of molecular diversity: a reappraisal. Molecular Ecology 18: 4541–4550.

Gaston, K.J.; Lawton, J.H. 1990. The population ecology of rare species. Journal of Fish Biology 37: 97–104.

Georgieva, M.N.; Wiklund, H.; Bell, J.B.; Eilertsen, M.H.; Mills, R.A.; Little, C.T.S.; et al. 2015. A chemosynthetic weed: the tubeworm Sclerolinum contortum is a bipolar, cosmopolitan species. BMC Evolutionary Biology 15.

Glasby, C.J.; Hutchings, P.A.; Fauchald, K.; Paxton, H.; Rouse, G.W.; Watson Russel, C.; et al. 2000. Class Polychaeta. In: Polychaetes & Allies: The Southern Synthesis,

Csiro Publishing, Melbourne, p.1–296.

Glaubrecht, M. 2007. Die Ordnung des Lebendigen. Zur Geschichte und Zukunft der Systematik in Deutschland. In: Höhepunkte Der Zoologischen Forschung Im Deutschen Sprachraum. Festschrift Zur 100. Jahresversammlung Der Deutschen Zoologischen Gesellschaft in K€oln., Basiliken Press, Marburg, p.59–110.

Glaubrecht, M. 2010. Evolutionssystematik limnischer Gastropoden. Habilitationsschrift zur Erlangung der Lehrbefähigung für das Fach Zoologie. Humboldt Universität, Berlin, .

Glover, A.; Dahlgren, T.; Wiklund, H.; Mohrbeck, I.; Smith, C. 2015. An End-to-End DNA Taxonomy Methodology for Benthic Biodiversity Survey in the Clarion-Clipperton Zone, Central Pacific Abyss. Journal of Marine Science and Engineering 4: 2.

Glover, A.; Paterson, G.; Bett, B.; Gage, J.; Myriam Sibuet; Sheader, M.; et al. 2001. Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 48: 217–236.

Glover, A.; Smith, C.; Paterson, G.; Wilson, G.; Hawkins, L.; Sheader, M. 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. Marine Ecology Progress Series 240: 157–170.

Glover, A.G.; Wiklund, H.; Chen, C.; Dahlgren, T.G. 2018. Managing a sustainable deep-sea 'blue economy' requires knowledge of what actually lives there. ELife 7.

Gonzalez, A.; Holt, R.D. 2002. The inflationary effects of environmental fluctuations in source-sink systems. Proceedings of the National Academy of Sciences 99: 14872–14877.

Gooday, A.J.; Hori, S.; Todo, Y.; Okamoto, T.; Kitazato, H.; Sabbatini, A. 2004. Soft-walled, monothalamous benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. Deep Sea Research Part I: Oceanographic Research Papers 51: 33–53.

Govenar, B. 2010. Shaping Vent and Seep Communities: Habitat Provision and Modification by Foundation Species. In: Kiel, S. (Ed.), The Vent and Seep Biota: Aspects from Microbes to Ecosystems, Springer Netherlands, Dordrecht, p.403–432.

Gower, J.; King, S. 2008. Satellite Images Show the Movement of Floating Sargassum in the Gulf of Mexico and Atlantic Ocean. Nature Precedings.

Grassle, J.F. 1989. Species diversity in deep-sea communities. Trends in Ecology & Evolution 4: 12–15.

Grassle, J.F.; Morse-Porteous, L.S. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep Sea Research Part A. Oceanographic Research Papers 34: 1911–1950.

Grassle, J.F.; Maciolek, N.J. 1992. Deep-Sea Species Richness: Regional and Local Diversity Estimates from Quantitative Bottom Samples. The American Naturalist 139: 313–341.

Gray, J. 2002. Species richness of marine soft sediments. Marine Ecology Progress Series 244: 285–297.

Grube, A.E. 1850. Die Familie der Anneliden. Archiv für Naturgeschichte 16: 294 364.

Harris, P.T. 2012. Seafloor Geomorphology—Coast, Shelf, and Abyss. In: Seafloor Geomorphology as Benthic Habitat, Elsevier, p.109–155.

Harris, P.T.; Macmillan-Lawler, M.; Rupp, J.; Baker, E.K. 2014. Geomorphology of the oceans. Marine Geology 352: 4–24.

Hartman, O. 1959. Catalogue of the Polychaetous Annelids of the World. Parts 1 and 2. Allan Hancock Foundation Occasional Paper: 1–628.

Hartman, O. 1965. Catalogue of the polychaetous annelids of the world: supplement, 1960–1965, and index. In: Allan Hancock Foundation Occasional Paper, Vol. 23, University of Southern California Press, Los Angeles, California, p.197 pp.

Hartmann-Schröder, G. 1996. Annelida, Borstenwürmer, Polychaeta. In: Die Tierwelt Deutschlands und der angrenzenden Meeresteile. 2., neubearbeitete Aufl ed. Gustav Fischer, Jena, 648p.

Herring, P. 2002. The Biology of the Deep Ocean. New ed. Oxford University Press, Oxford ; New York, 326p.

Hessler, R.; Sanders, H. 1967. Faunal diversity in the deep-sea. Deep Sea Research and Oceanographic Abstracts 14: 65–78.

Higgs, N.D.; Attrill, M.J. 2015. Biases in biodiversity: wide-ranging species are discovered first in the deep sea. Frontiers in Marine Science 2.

Hilário, A.; Metaxas, A.; Gaudron, S.M.; Howell, K.L.; Mercier, A.; Mestre, N.C.; et al. 2015. Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Frontiers in Marine Science 2.

Hilbig, B.; Blake, J.A. 2006. Deep-sea polychaete communities in the northeast Pacific Ocean off the Gulf of the Farallones, California. Bulletin of Marine Science 78: 27.

Hutchings, P.; Peart, R. 2000. A revision of the Australian Trichobranchidae (Polychaeta). Invertebrate Systematics 14: 225–272.

Hutchings, P.; Kupriyanova, E. 2018. Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives. Invertebrate Systematics 32: 1.

Hutchings, P.A.; Glasby, C.J. 1991. Phylogenetic Implications of the Biogeography of Australian Terebellidae (Polychaeta). Ophelia: 565–572.

Jamieson, A. 2015. The Hadal Zone by Alan Jamieson. .

Jamieson, A.J.; Fujii, T.; Mayor, D.J.; Solan, M.; Priede, I.G. 2010. Hadal trenches: the ecology of the deepest places on Earth. Trends in Ecology & Evolution 25: 190–197.

Jumars, P.A.; Dorgan, K.M.; Lindsay, S.M. 2015. Diet of Worms Emended: An Update of Polychaete Feeding Guilds. Annual Review of Marine Science 7: 497–520.

Kingsford, M.J.; Leis, J.M.; Shanks, A.; Lindeman, K.C.; Morgan, S.G.; Pineda, J. 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70: 33.

Kunin, W.E.; Gaston, K.J. 2012. The Biology of Rarity: Causes and consequences of rare—common differences. Springer Science & Business Media, 291p.

Lambshead, P.; Tietjen, J.; Ferrero, T.; Jensen, P. 2000. Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. Marine Ecology Progress Series 194: 159–167.

Leduc, D.; Rowden, A.A.; Probert, P.K.; Pilditch, C.A.; Nodder, S.D.; Vanreusel, A.; et al. 2012. Further evidence for the effect of particle-size diversity on deep-sea benthic biodiversity. Deep Sea Research Part I: Oceanographic Research Papers 63: 164–169.

Lemche, H.; Hansen, B.; Madsen, F.J.; Tendal, O.; Wolff, T. 1976. Hadal life as analyzed from photographs. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 139: 263–336.

Lester, S.E.; Ruttenberg, B.I.; Gaines, S.D.; Kinlan, B.P. 2007. The relationship between dispersal ability and geographic range size. Ecology Letters 10: 745–758.

Levin, L.A.; Gooday, A.J. 2003. The deep Atlantic Ocean. In: Tyler, P.A. (Ed.), Ecosystems of the World, Vol. 28. Ecosystems of the Deep Oceans, Elsevier, p.111–178.

Lins, L.; Derycke, S.; Campinas, T.B.; Vanreusel, A. 2018b. Do physical barriers hamper dispersal in the deep sea? PeerJ Preprint 6.

Lins, L.; da Silva, M.C.; Neres, P.; Esteves, A.M.; Vanreusel, A. 2018a. Testing deep-sea biodiversity paradigms on abyssal nematode genera and Acantholaimus species. Deep Sea Research Part II: Topical Studies in Oceanography 148: 208–222.

Linse, K.; Schwabe, E. 2018. Diversity of macrofaunal Mollusca of the abyssal Vema Fracture Zone and hadal Puerto Rico Trench, Tropical North Atlantic. Deep Sea Research Part II: Topical Studies in Oceanography 148: 45–53.

Linse, K.; Brandt, A.; Bohn, J.M.; Danis, B.; De Broyer, C.; Ebbe, B.; et al. 2007. Macro- and megabenthic assemblages in the bathyal and abyssal Weddell Sea (Southern Ocean). Deep Sea Research Part II: Topical Studies in Oceanography 54: 1848–1863.

Lyons, K.G.; Brigham, C.A.; Traut, B.H.; Schwartz, M.W. 2005. Rare Species and Ecosystem Functioning: Rare Species and Ecosystem Functioning. Conservation Biology 19: 1019–1024.

MacDonald, I.R.; Bluhm, B.A.; Iken, K.; Gagaev, S.; Strong, S. 2010. Benthic macrofauna and megafauna assemblages in the Arctic deep-sea Canada Basin. Deep Sea Research Part II: Topical Studies in Oceanography 57: 136–152.

Maciolek, N.J. 1981a. Spionidae (Annelida: Polychaeta) from the Galapagos Rift geothermal vents. Proceedings of The Biological Society of Washington 94.3: 826–837.

Magurran, A.E.; Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422: 714–716.

Martin, D.; Britayev, T.A. 1998. Symbiotic polychaetes: review of known. Oceanography and Marine Biology : an annual review.

Mauritzen, C. 2002. Evidence in hydrography and density fine structure for enhanced vertical mixing over the Mid-Atlantic Ridge in the western Atlantic. Journal of Geophysical Research 107.

McCartney, M.S.; Bennett, S.L.; Woodgate-Jones, M.E. 1991. Eastward Flow through the Mid-Atlantic Ridge at 11°N and Its Influence on the Abyss of the Eastern Basin. Journal of Physical Oceanography 21: 1089–1121.

McClain, C.R.; Hardy, S.M. 2010. The dynamics of biogeographic ranges in the deep sea. Proceedings of the Royal Society B: Biological Sciences 277: 3533–3546.

McClain, C.R.; Schlacher, T.A. 2015. On some hypotheses of diversity of animal life at great depths on the sea floor. Marine Ecology 36: 849–872.

McClain, C.R.; Allen, A.P.; Tittensor, D.P.; Rex, M.A. 2012. Energetics of life on the deep seafloor. Proceedings of the National Academy of Sciences 109: 15366–15371.

Meißner, K.; Blank, M. 2009. Spiophanes norrisi sp. nov. (Polychaeta: Spionidae) a new species from the NE Pacific coast, separated from the Spiophanes bombyx com-

plex based on both morphological and genetic studies. Zootaxa 2278: 1–25.

Metaxas, A.; Saunders, M. 2009. Quantifying the “Bio-” Components in Biophysical Models of Larval Transport in Marine Benthic Invertebrates: Advances and Pitfalls. The Biological Bulletin 216: 257–272.

Mincks, S.L.; Dyal, P.L.; Paterson, G.L.J.; Smith, C.R.; Glover, A.G. 2009. A new species of Aurospio (Polychaeta, Spionidae) from the Antarctic shelf, with analysis of its ecology, reproductive biology and evolutionary history. Marine Ecology 30: 181–197.

Moreno, R.A.; Rivadeneira, M.M.; Hernández, C.E.; Sampértegui, S.; Rozbaczylo, N. 2008. Do Rapoport’s rule, the mid-domain effect or the source-sink hypotheses predict bathymetric patterns of polychaete richness on the Pacific coast of South America? Global Ecology and Biogeography 17: 415–423.

Moritz, C.; Cicero, C. 2004. DNA Barcoding: Promise and Pitfalls. PLoS Biology 2: e354.

Murray, J.; Hjort, J. 1912. Depths of the Ocean. .

Neal, L.; Wiklund, H.; Muir, A.I.; Linse, K.; Glover, A.G. 2014. The identity of juvenile Polynoidae (Annelida) in the Southern Ocean revealed by DNA taxonomy, with notes on the status of Herdmanella gracilis Ehlers sensu Augener. Memoirs of Museum Victoria 71: 203–216.

Norkko, A.; Rosenberg, R.; Thrush, S.F.; Whitlatch, R.B. 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. Journal of Experimental Marine Biology and Ecology 330: 195–207.

Nowell, A.R.M.; Jumars, P.A.; Fauchald, K. 1984. The foraging strategy of a subtidal and deep-sea deposit feeder1. Limnology and Oceanography 29: 645–649.

Nygren, A. 2014. Cryptic polychaete diversity: a review. Zoologica Scripta 43: 172–183.

Nygren, A.; Parapar, J.; Pons, J.; Meißner, K.; Bakken, T.; Kongsrud, J.A.; et al. 2018. A mega-cryptic species complex hidden among one of the most common annelids in the North East Atlantic. PLOS ONE 13: e0198356.

O’Connor, M.I.; Bruno, J.F.; Gaines, S.D.; Halpern, B.S.; Lester, S.E.; Kinlan, B.P.; et al. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proceedings of the National Academy of Sciences 104: 1266–1271.

Pamungkas, J.; Glasby, C.J.; Read, G.B.; Wilson, S.P.; Costello, M.J. 2019. Progress and perspectives in the discovery of polychaete worms (Annelida) of the world. Helgoland Marine Research 73.

Parapar, J.; Hutchings, P.A. 2015. Redescription of Terebellides stroemii (Polychaeta, Trichobranchidae) and designation of a neotype. Journal of the Marine Biological Association of the United Kingdom 95: 323–337.

Paterson, G.L.J.; Wilson, G.D.F.; Cosson, N.; Lamont, P.A. 1998. Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. Deep Sea Research Part II: Topical Studies in Oceanography 45: 225–251.

Paterson, G.L.J.; Glover, A.G.; Barrio Froján, C.R.S.; Whitaker, A.; Budaeva, N.; Chimonides, J.; et al. 2009. A census of abyssal polychaetes. Deep Sea Research Part II: Topical Studies in Oceanography 56: 1739–1746.

Paterson, G.L.J.; Neal, L.; Altamira, I.; Soto, E.H.; Smith, C.R.; Menot, L.; et al. 2016. New Prionospio and Aurospio Species from the Deep Sea (Annelida: Polychaeta). Zoo-

taxa 4092: 1.

Paulay, G.; Meyer, C. 2006. Dispersal and divergence across the greatest ocean region: Do larvae matter? Integrative and Comparative Biology 46: 269–281.

Pineda, J.; Reyns, N.B.; Starczak, V.R. 2009. Complexity and simplification in understanding recruitment in benthic populations. Population Ecology 51: 17–32.

Polzin, K.L. 1997. Spatial Variability of Turbulent Mixing in the Abyssal Ocean. Science 276: 93–96.

Polzin, K.L.; Speer, K.G.; Toole, J.M.; Schmitt, R.W. 1996. Intense mixing of Antarctic Bottom Water in the equatorial Atlantic Ocean. Nature 380: 54.

Quatrefages, A.D. 1865. Note sur la classification des Annélides. Comptes rendus des séances de l'Académie des Sciences 60: 586–600.

Ramirez-Llodra, E.; Brandt, A.; Danovaro, R.; De Mol, B.; Escobar, E.; German, C.R.; et al. 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7: 2851–2899.

Read, J.F.; Pollard, R.T.; Miller, P.I.; Dale, A.C. 2010. Circulation and variability of the North Atlantic Current in the vicinity of the Mid-Atlantic Ridge. Deep Sea Research Part I: Oceanographic Research Papers 57: 307–318.

Rex, M. 2002. Biogeography of the deep-sea gastropod Palazzia planorbis (Dall, 1927): an uncommon form of rarity. Nautilus -Greenville then Sanibel- 116: 36–38.

Rex, M.; Etter, R.; Morris, J.; Crouse, J.; McClain, C.; Johnson, N.; et al. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Marine Ecology Progress Series 317: 1–8.

Rex, M.A. 1981. Community Structure in the Deep-Sea Benthos. Annual Review of Ecology and Systematics 12: 331–353.

Rex, M.A.; Etter, R.J. 2010. Deep-sea Biodiversity: Pattern and Scale. Harvard University Press, 388p.

Rex, M.A.; Stuart, C.T.; Coyne, G. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proceedings of the National Academy of Sciences 97: 4082–4085.

Rex, M.A.; Etter, R.J.; Stuart, C.T.; Tickell, C. 1997. Large-scale patterns of species diversity in the deep-sea benthos. In: Ormond, R.F.G.; Gage, J.D.; Angel, M.V. (Eds.), Marine Biodiversity, Cambridge University Press, Cambridge, p.94–121.

Rex, M.A.; Stuart, C.T.; Hessler, R.R.; Allen, J.A.; Sanders, H.L.; Wilson, G.D.F. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365: 636.

Rex, M.A.; McClain, C.R.; Johnson, N.A.; Etter, R.J.; Allen, J.A.; Bouchet, P.; et al. 2005. A Source□Sink Hypothesis for Abyssal Biodiversity. The American Naturalist 165: 163–178.

Richardson, M.D.; Briggs, K.B.; Bowles, F.A.; Tietjen, J.H. 1995. A depauperate benthic assemblage from the nutrient-poor sediments of the Puerto Rico Trench. Deep Sea Research Part I: Oceanographic Research Papers 42: 351–364.

Riehl, T.; Kaiser, S.; Brandt, A. 2018a. Vema-TRANSIT – An interdisciplinary study on the bathymetry of the Vema-Fracture Zone and Puerto Rico Trench as well as abyssal Atlantic biodiversity. Deep Sea Research Part II: Topical Studies in Oceanography 148:

1–6.

Riehl, T.; Lins, L.; Brandt, A. 2018b. The effects of depth, distance, and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostylidae). Deep Sea Research Part II: Topical Studies in Oceanography 148: 74–90.

Robison, B.H. 2004. Deep pelagic biology. Journal of Experimental Marine Biology and Ecology 300: 253–272.

Rogacheva, A.; Gebruk, A.; Alt, C.H.S. 2012. Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge. Zoosymposia 7: 213–224.

Romankevich, E.A.; Vetrov, A.A.; Peresypkin, V.I. 2009. Organic matter of the World Ocean. Russian Geology and Geophysics 50: 299–307.

Sanders, H.L.; Hessler, R.R. 1969. Ecology of the Deep-Sea Benthos. Science 163: 1419–1424.

Scheltema, R.S. 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary. In: Brauer, R.W. (Ed.), Barobiology and the Experimental Biology of the Deep Sea, University of North Carolina, Chapel Hill, p.58–66.

Scheltema, R.S. 1994. Adaptations for reproduction among deep-sea benthic molluscs: an appraisal. In: Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos, p.44–75.

Schüller, M. 2011. Evidence for a role of bathymetry and emergence in speciation in the genus Glycera (Glyceridae, Polychaeta) from the deep Eastern Weddell Sea. Polar Biology 34: 549–564.

Schüller, M.; Ebbe, B. 2007. Global distributional patterns of selected deep-sea Polychaeta (Annelida) from the Southern Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 54: 1737–1751.

Schüller, M.; Hutchings, P.A. 2012. New species of Terebellides (Polychaeta: Trichobranchidae) from the deep Southern Ocean, with a key to all described species. Zootaxa 3619: 1–31.

Schüller, M.; Ebbe, B.; Wägele, J.-W. 2009. Community structure and diversity of polychaetes (Annelida) in the deep Weddell Sea (Southern Ocean) and adjacent basins. Marine Biodiversity 39: 95–108.

Schwentner, M.; Timms, B.V.; Richter, S. 2014. Evolutionary systematics of the Australian Eocyzicus fauna (Crustacea: Branchiopoda: Spinicaudata) reveals hidden diversity and phylogeographic structure. Journal of Zoological Systematics and Evolutionary Research 52: 15–31.

Shanks, A.L. 2009. Pelagic Larval Duration and Dispersal Distance Revisited. The Biological Bulletin 216: 373–385.

Shields, M.A.; Blanco-Perez, R. 2013. Polychaete abundance, biomass and diversity patterns at the Mid-Atlantic Ridge, North Atlantic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 98: 315–325.

Sibuet, M.; E. Lambert, C.; Chesselet, R.; Laubier, L. 1989. Density of major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. Journal of Marine Research 47: 851–867.

Sikorski, A.; Pavlova, L. 2016. Three new species of Laonice (Polychaete: Spionidae) from West and Southwest Africa. Zootaxa 4097: 353–368.

Sikorski, A.; Gunton, L.M.; Pavlova, L. 2017. Laonice species (Polychaeta, Spionidae) from the Whittard Canyon (NE Atlantic) with descriptions of two new species. Journal of the Marine Biological Association of the United Kingdom 97: 961–973.

Sikorski, A.V. 2003. Laonice (Polychaeta, Spionidae) in the Arctic and the North Atlantic. Sarsia 88: 316–345.

Smith, C.; Deleo, F.; Bernardino, A.; Sweetman, A.; Arbizu, P. 2008. Abyssal food limitation, ecosystem structure and climate change. Trends in Ecology & Evolution 23: 518–528.

Smith, C.R.; Demopoulos, A.W.J. 2003. The deep Pacific Ocean floor. In: Ecosystems of the Deep Oceans, Elsevier, Amsterdam, p.179–218.

Snelgrove, P.V.; Smith, C.R. 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. In: Oceanography and Marine Biology, An Annual Review, Volume 40, Vol. 40, p.311–342.

Snelgrove, P.V.R. 1997. The Importance of Marine Sediment Biodiversity in Ecosystem Processes. Ambio 26: 578–583.

Stow, D.A.V.; Faugères, J.-C.; Howe, J.A.; Pudsey, C.J.; Viana, A.R. 2002. Bottom currents, contourites and deep-sea sediment drifts: current state-of-the-art. Geological Society, London, Memoirs 22: 7–20.

Struck, T.H.; Paul, C.; Hill, N.; Hartmann, S.; Hösel, C.; Kube, M.; et al. 2011. Phylogenomic analyses unravel annelid evolution. Nature 471: 95–98.

Stuart, C.T.; Brault, S.; Rowe, G.T.; Wei, C.-L.; Wagstaff, M.; McClain, C.R.; et al. 2017. Nestedness and species replacement along bathymetric gradients in the deep sea reflect productivity: a test with polychaete assemblages in the oligotrophic north-west Gulf of Mexico. Journal of Biogeography 44: 548–555.

Taylor, M.L.; Roterman, C.N. 2017. Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. Molecular Ecology 26: 4872–4896.

Thistle, D. 2003. Chapter 2 The Deep-sea floor: an overview. In: Ecosystems of the Deep Oceans, Elsevier,.

Tunnicliffe, V.; Juniper, S.K.; Sibuet, M. 2003. Reducing environments of the deep-sea floor. In: Ecosystems of the Deep Oceans, Elsevier, Amsterdam, p.81–110.

Turner, J.P.; Rooker, J.R. 2006. Fatty acid composition of flora and fauna associated with Sargassum mats in the Gulf of Mexico. Marine Biology 149: 1025–1036.

Tyler, P.A. 1980. Deep-sea Ophiuroids. Oceanography and Marine Biology. An Annual Review. 18: 125–153.

Tyler, P.A. 1988. Seasonality in the deep sea. Oceanogr.Mar.Biol.Ann.Rev. 26: 227–258.

Tyler, P.A.; Young, C.M. 1998. Temperature and pressure tolerances in dispersal stages of the genus Echinus (Echinodermata: Echinoidea): prerequisites for deep-sea invasion and speciation. Deep Sea Research Part II: Topical Studies in Oceanography 45: 253–277.

Van Andel, T.H.; Von Herzen, R.P.; Phillips, J.D. 1971. The Vema fracture zone and the tectonics of transverse shear zones in oceanic crustal plates. Marine Geophysical Researches 1: 261–283.

Van Dover, C.L. 2002. Evolution and Biogeography of Deep-Sea Vent and Seep Inver-

tebrates. Science 295: 1253–1257.

Vanreusel, A.; Fonseca, G.; Danovaro, R.; Silva, M.C.D.; Esteves, A.M.; Ferrero, T.; et al. 2010. The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. Marine Ecology 31: 6–20.

Vrijenhoek, R.C. 2009. Cryptic species, phenotypic plasticity, and complex life histories: Assessing deep-sea faunal diversity with molecular markers. Deep Sea Research Part II: Topical Studies in Oceanography 56: 1713–1723.

Washington, H.G. 1984. Diversity, biotic and similarity indices: A review with special relevance to aquatic ecosystems. Water Research 18: 653–694.

Weigert, A.; Bleidorn, C. 2016. Current status of annelid phylogeny. Organisms Diversity & Evolution 16: 345–362.

Weigert, A.; Helm, C.; Meyer, M.; Nickel, B.; Arendt, D.; Hausdorf, B.; et al. 2014. Illuminating the Base of the Annelid Tree Using Transcriptomics. Molecular Biology and Evolution 31: 1391–1401.

Weigert, A.; Golombek, A.; Gerth, M.; Schwarz, F.; Struck, T.H.; Bleidorn, C. 2016. Evolution of mitochondrial gene order in Annelida. Molecular Phylogenetics and Evolution 94: 196–206.

Wheeler, Q. 2018. Blank Canvas: The Case for Descriptive Taxonomy. Integrative and Comparative Biology 58: 1118–1121.

Will, K.W.; Mishler, B.D.; Wheeler, Q.D. 2005. The Perils of DNA Barcoding and the Need for Integrative Taxonomy. Systematic Biology 54: 844–851.

Willette, D.; Allendorf, F.; Barber, P.; Barshis, D.; Carpenter, K.; Crandall, E.; et al. 2014. So, you want to use next-generation sequencing in marine systems? Insight from the Pan-Pacific Advanced Studies Institute. Bulletin of Marine Science 90: 79–122.

Williams, S.J. 1984. The status of Terebellides stroemii (Polychaeta, Trichobranchidae) as a cosmopolitan species on a worldwide morphological survey, including description of a new species. Proceedings of 1st International Polychaete Conference: 118–142.

Wilson, G.D.F. 2017. Macrofauna abundance, species diversity and turnover at three sites in the Clipperton-Clarion Fracture Zone. Marine Biodiversity 47: 323–347.

Wilson, W.H. 1990. Competition and Predation in Marine Soft-Sediment Communities. Annual Review of Ecology and Systematics 21: 221–241.

Wilson, W.H. 1991. Sexual reproductive modes in polychaetes: classification and diversity. Bulletin of Marine Science 48: 17.

Wolff, T. 1979. Magrofaunal utilization of plant remains in the deep sea. Sarsia 64: 117–143.

Yearsley, J.M.; Sigwart, J.D. 2011. Larval Transport Modeling of Deep-Sea Invertebrates Can Aid the Search for Undiscovered Populations. PLoS ONE 6: e23063.

Young, C. 2003. Reproduction, development and life-history traits. In: Ecosystems of the World, Elsevier Science, Amsterdam, p.381–426.

Young, C.M. 2009. Communities on Deep-Sea Hard Bottoms. In: Wahl, M. (Ed.), Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change, Springer Berlin Heidelberg, Berlin, Heidelberg, p.39–60.

Young, C.M.; Eckelbarger, K.J.; Eckelbarger, K. 1994. Reproduction, Larval Biology,