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Testing deep-sea biodiversity paradigms on abyssal nematode genera and *Acantholaimus* species

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ABSTRACT

Biodiversity patterns in the deep sea have been extensively studied in the last decades. In this study, we investigated whether reputable concepts in deep-sea ecology also explain diversity and distribution patterns of nematode genera and species in the abyss. Among them, three paradigms were tackled: (1) the deep sea is a highly diverse environment at a local scale, while on a regional and even larger geographical scale, species and genus turnover is limited; (2) the biodiversity of deep-sea nematode communities changes with the nature and amount of organic matter input from the surface; and (3) patch-mosaic dynamics of the deep-sea environment drive local diversity. To test these hypotheses, diversity and density of nematode assemblages and of species of the genus *Acantholaimus* were studied along two abyssal E-W transects. These two transects were situated in the Southern Ocean (~50°S) and the North Atlantic (~10°N). Four different hierarchical scales were used to compare biodiversity: at the scale of cores, between stations from the same region, and between regions. Results revealed that the deep sea harbours a high diversity at a local scale (alpha diversity), but that turnover can be shaped by different environmental drivers. Therefore, these results question the second part of the paradigm about limited species turnover in the deep sea. Higher surface primary productivity was correlated with greater nematode densities, whereas diversity responses to the augmentation of surface productivity showed no trend. Areas subjected to a constant and low food input revealed similar nematode communities to other oligotrophic abyssal areas, while stations under high productivity were characterized by different dominant genera and *Acantholaimus* species, and by a generally low local diversity. Our results corroborate the species-energy hypothesis, where productivity can set a limit to the richness of an ecosystem. Finally, we observed no correlation between sediment variability and local diversity. Although differences in sediment variability were significant across stations, these had to be considered without effect on the nematode community structure in the studied abyssal areas.

1. Introduction

Recent advances in deep-sea research have tested established paradigms of deep-sea diversity (McClain and Schlacher, 2015). Among them, productivity effects on benthic diversity, patch-mosaic dynamics structuring assemblages, and the high local diversity encountered in the deep sea have been discussed extensively (Gage, 1996; Grassle and Sanders, 1973; Lambshead and Boucher, 2003; Levin et al., 2001; McClain and Schlacher, 2015). The increasing interest in ecosystem functioning and ecosystem services and their relation to biodiversity has not only brought new insights on the interactions between abiotic and biotic elements of different habitats, but also on carbon sequestration and burial in the deep sea (Levin and Dayton, 2009; Thurber et al., 2014). Nevertheless, to provide information about functions and services of an ecosystem, background evidence on the ecosystem structure is essential to understand the consequences of biodiversity loss (Danovaro et al., 2008; Frid and Caswell, 2016; Thurber et al., 2014).

Reduced diversity may lead to a reduction of functions in an ecosystem (Danovaro et al., 2008; Thurber et al., 2014). However, particularly for small-sized taxa, such as those comprising the meiofauna, deep-sea species remain largely undescribed (Ramirez-Llodra et al., 2010), hampering estimates of diversity and consequently the costs of biodiversity loss. Nematodes, which frequently represent more

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than 90% of the meiofauna, are considered to be rich in species in the deep sea (Danovaro et al., 2010; Mokievskii et al., 2007). Due to the time-consuming investment required for describing new species, effort in nematode taxonomic identification, especially towards macro-ecological approaches, is often limited to genus level (Ingels et al., 2011; Netto et al., 2005; Pape et al., 2013b; Sebastian et al., 2007; Somerfield and Clarke, 1995; Vanreusel et al., 2010). For investigating ecological concepts and the effect of environmental factors on nematode biodiversity, identification down to genus level seems to be sufficient, as most deep-sea nematode genera have low environmental specificity (Leduc et al., 2012a). Nevertheless, the lack of species-level information can restrict comparisons between studies in terms of species distribution and biodiversity estimates. In general, the wide distribution, higher diversity, and higher abundances of nematodes in the deep sea, compared to other metazoan organisms (Brandt et al., 2014; Danovaro et al., 2010; Rex et al., 2006), support them as an ideal group to tackle paradigms of deep-sea biodiversity.

This study aimed to test whether the mentioned paradigms of deep-sea biodiversity can also be applied for nematode communities. The first paradigm tested in this study (1) refers to the deep sea (> 1000 m) as a highly diverse environment at a local scale (alpha diversity), while turnover (beta diversity) is limited (Lambshead and Boucher, 2003). Presently, few species-level comparisons support this statement (Gray, 2002, 1994; Hessler and Sanders, 1968, 1967; Rex et al., 1993; Sanders et al., 1965; Sanders and Hessler, 1969), and the subject has raised new discussions in recently published papers, where diversity varies according to different spatial scales (Bik et al., 2010; Levin et al., 2001; McClain and Schlacher, 2015; Snelgrove and Smith, 2002). For deep-sea nematodes, for example, a high local alpha diversity is inferred, while regional beta diversity would change moderately (Lambshead, 2004; Lambshead and Boucher, 2003; Mokievskii et al., 2007). In this sense, it is important to consider at which spatial scale (alpha or beta) biodiversity is measured and compared. The second paradigm, (2) relies on how surface primary productivity regulates diversity at a local scale (Gooday, 2002; McClain and Schlacher, 2015; Moens et al., 2014; Snelgrove and Smith, 2002). Seasonal variation and geographical patterns in primary productivity are known to influence the flux of organic matter to the seafloor and consequently the organic matter uptake by the benthic biota (Gooday, 2002; Moodley et al., 2002). Moreover, regions under eutrophic conditions, mostly present at high latitude or in temperate environments, have shown to exhibit a stronger seasonal benthic-pelagic coupling in comparison with oligotrophic areas (Gooday, 2002; Smith et al., 2008; Wei et al., 2010). Usually, oligotrophic regions at lower latitudes exhibit weak seasonal signals, which are reflected in the small diatom cell production and slow sinking rates (Gooday, 2002). The resulting lower benthic standing stocks observed with increasing depth, e.g. in the abyss, where undisturbed muddy-sediment conditions predominate, is mainly the result of the low organic matter input in these areas (Lambshead et al., 2002; Woolley et al., 2016). For nematodes, higher local alpha diversity was observed under more productive regions in the abyss (Lambshead et al., 2002; Sebastian et al., 2007), but negative or no trends were also reported (Lambshead et al., 2000). Nevertheless, these observed positive or negative relationships might only be a reflection of part of a unimodal productivity-diversity distribution with maximum diversity at intermediate productivity (Leduc et al., 2012b). Therefore, organic matter input may be a limiting factor at its low and high extremes, where niche diversification and reduced species interactions can be favoured in one end, while species dominance can be enhanced in the other end (Leduc et al., 2012b; Snelgrove and Smith, 2002). A third deep-sea paradigm is based on the (3) patch-mosaic hypothesis and the idea that patchiness has a positive effect on the structure of benthic assemblages (Grassle and Sanders, 1973). Patchiness, or microhabitats, can include for e.g. spatially localized or temporally pulsed food input. In addition, sediment heterogeneity can also be responsible for the concentration of organic matter in localised patches (Levin et al., 2001). For nematodes, small-scale patchiness (i.e. patchiness at the level of station replicates) is considered imperative in determining their settling conditions more than large geographical distances (Ingels and Vanreusel, 2013). Together with food input, sediment particle-size diversity is considered to increase spatial-scale heterogeneity and consequently enhance nematode diversity through the increase in partitioning of food resources (Leduc et al., 2012c). In this case, one would expect that both food input and sediment heterogeneity would contribute to higher patchiness, and consequently to a positive effect on the nematode species beta diversity.

The genus *Acantholaimus* Allgén, 1933 is generally found in high diversity in different deep-sea environments worldwide (De Mesel et al., 2006; Muthumbi and Vincx, 1997; Vanreusel et al., 2010). *Acantholaimus* is one of the most abundant nematode genera in abyssal plains (Lins et al., 2015; Miljutina et al., 2010; Sebastian et al., 2007; Singh et al., 2014), while it is only rare at coastal or shelf habitats (Vanreusel et al., 2010). Represented by 51 described species at present, this diverse genus increases in relative abundance with increasing water depth and possesses a large morphological variation, making it a highly suitable group for biodiversity comparison under different productivity regimes and at different spatial scales (Miljutin and Miljutina, 2016a). Although specific information on the trophic ecology of *Acantholaimus* is still lacking, other studied species from the same family, though from different genera, show a diatom-feeding behaviour (Jensen, 1987, 1982; Moens and Vincx, 1997). In this regard, since eutrophic regions are characterized by a higher fresh food input (e.g. increased sinking of diatoms) to the benthos, they may consequently favour species establishment and diversity of this genus (De Mesel et al., 2006). Nevertheless, the success of *Acantholaimus* in the most food-depleted environments, such as the abyss, contrasts with this assumption.

The aim of this study was to investigate whether the paradigms of biodiversity stated above can be applied for nematodes in this study and elsewhere. Paradigm (1), the deep sea is diverse at a local scale but turnover is limited, was tested by comparing alpha (α) diversity (i.e. diversity at the scale of core) of nematode genera with beta (β) diversity at increasing spatial scale through additive partitioning, where the contribution of each level (α and β) was brought to the same scale. Furthermore, data on species distribution of the nematode genus *Acantholaimus* collected in this study was combined with available literature data. Because the study areas comprised two comparable abyssal transects (Southern Ocean and southern North Atlantic) under different surface productivity regimes (seasonal eutrophic and oligotrophic areas, respectively), the second paradigm (2) on benthic-pelagic coupling, surface primary production and its role in regulating nematode alpha diversity could be tested. Differences in genus and species diversity were correlated with differences in surface productivity between stations and regions. The third paradigm, (3) patch–mosaic dynamics structuring nematode communities, was supported by linking spatial changes in benthic environmental variables at a local scale (e.g. sediment particle size diversity and organic matter input within a station) to the observed nematode genus composition and *Acantholaimus* species diversity.

2. Material and methods

2.1. Sampling and study area

The studied areas comprised four stations (four replicates per station) in the Southern Ocean (SO) and six stations (three replicates per station except for one station (B1) with two replicates) in the North Atlantic (NA) (Fig. 1). Sediment samples were collected on board of the RV Polarstern (ANT-XXVIII/3, 07.01.2012–11.03.2012) and RV Sonne (SO 237, 14.12.2014–26.01.2015), respectively. The SO transect was located at the Polar Front along an E-W gradient (between 10°E and 39°W), and covered depths from 3760.5 m to 4155.2 m (Table 1).

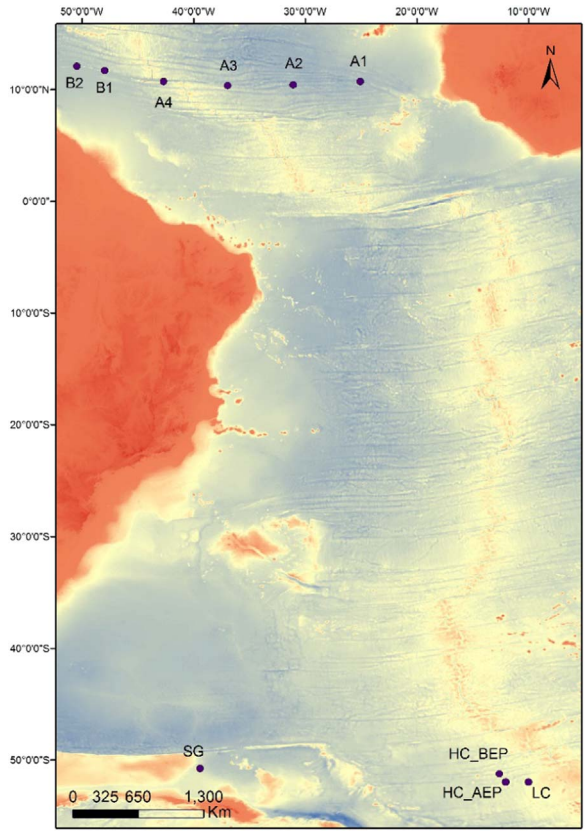

Fig. 1. Location of ANT-XXVIII/3 and SO 237 stations. Exact coordinates are given in Table 1. Bathymetry data was provided by GEBCO. Sampling stations are represented by symbols: SG (South Georgia), HC_BEP (High Chlorophyll_Before Eddy Pump), HC_AEP (High Chlorophyll_After Eddy Pump), LC (Low Chlorophyll); A1, A2, and A3 (East Mid-Atlantic Ridge), A4 (at the Mid-Atlantic Ridge), and B1, B2 (West of the Mid-Atlantic Ridge).

The NA transect sampling sites were situated at the Vema fracture zone along an E-W gradient (between 25 °W and 50 °W), comprising depths from 4998.3 m to 5771.7 m (Table 1). The SO stations were less evenly spread compared to the NA stations. However, both covered more than 2700 km from one end to the other, while the distance between stations varied from 90 km to 1800 km. Both samplings were performed using a Multicorer (MUC) equipped with 12 plexiglass tubes yielding samples with a virtually undisturbed sediment-surface (cross-sectional area of 25.5 cm² for ANT-XXVIII/3 and of 69.4 cm² for SO 237).

Along the SO transect (Wolf-Gladrow, 2012), there was a decrease in surface Chlorophyll *a* (Chla), with the most westward station South Georgia (SG), located northwest of South Georgia island, exhibiting higher surface Chla values (Lins et al., 2015). South Georgia island and its surroundings are considered a highly productive region during austral summer, supporting high phytoplankton biomass (Atkinson et al., 2001). The second and third stations, HC_BEP (High Chlorophyll_Before Eddy Pump) and HC_AEP (High Chlorophyll_After Eddy Pump), are located at the same area (stations are situated ~90 km apart) which was resampled after 13 days of a phytoplankton bloom. Despite a higher concentration of Chla was expected after the bloom, these differences could not be observed in the surface Chla maps. The station names (before and after eddy pump) are derived from eddies (anomalies) observed after the first station (HC_BEP) was sampled. Additionally, the two last stations (HC_BEP and HC_AEP) are also characterized by a high surface annual productivity. The easternmost station (LC; Low Chlorophyll), exhibited low surface Chla values throughout the whole year. The sampled stations were located in the Subantarctic Water Ring Province (SANT), and more specifically at the Polar Front Zone, where algal growth is enhanced and chlorophyll accumulates mainly during early austral fall (Longhurst, 1998).

The NA sampling comprised stations along the Vema fracture zone. The first three stations (A1, A2, and A3) were situated east of the Mid-Atlantic Ridge (MAR), one station was sampled at the central valley of the MAR (A4), and two other stations west of the MAR (B1 and B2). The sampled stations are located in the North Atlantic Tropical Gyral Province (NATR). This region lies below the North Atlantic trades and is separated from the westerlies by the Azores High (Longhurst, 1998). Moreover, the NATR exhibits low and uniform surface chlorophyll values, with weak winter convective mixing and no evidence of a spring bloom (Jochem and Zeitzschel, 1993).

2.2. Environmental variables

Samples for granulometric and geochemical analyses (1 g of sediment) were obtained from MUC deployments from the first sediment layer (0–1 cm) and were frozen at -80 °C. Replicates used for environmental analyses can be found in Table 1. Grain-size distribution was measured with a Malvern Mastersizer 2000 (0.02–2000 μm size range) and divided into five categories, from silt-clay to coarse sand fractions. Sediment particle-size diversity (SED) was calculated from the percent dry weight of the five size classes mentioned above using the Shannon-Wiener diversity index (Etter and Grassle, 1992; Leduc et al., 2012c). Total sedimentary organic carbon (% TOC) and nitrogen (% TN) were determined with a Carlo Erba elemental analyser on the freeze-dried and homogenized samples after acidification with 1% HCl until carbonates are removed (2–3 days). Total organic matter (% TOM) content was determined after combustion of the sediment samples at 550 °C.

Chla, chlorophyll degradation products, and carotenoids in the sediment were measured with a Gibson fluorescence detector (Wright and Jeffrey, 1997) after lyophilisation, homogenization, and extraction in 90% acetone. Separation of the samples occurred via reverse-phase HPLC (High-Performance Liquid Chromatography). Chloroplastic pigment equivalents (CPE: Chla + phaeopigments) were used as a proxy for surface-derived primary productivity at the seafloor.

Net primary productivity (NPP) values were extracted from the Vertically Generalized Production Model (VGPM; resolution 1°) described by Behrenfeld and Falkowski (1997) and explained in detail by Lins et al. (2014). The extracted NPP values corresponded to the average between the sampled month and the month before. Monthly NPP were calculated in order to investigate seasonality of primary productivity within a year between the different sampled regions.

2.3. Nematode sampling processing

At each station two to four replicates (cores) from 0–1 sediment layer were used for nematode analyses (Table 1). They were fixed in sea-water buffered formalin 4%, then washed using stacked sieves of 1000 μm and 32 μm, followed by three times centrifugation with Ludox HS40 Dupont (specific gravity 1.18). By using the 1000 μm sieve, the meiofauna could be separated from the macrofauna organisms. Subsequently, nematodes were counted under a stereomicroscope (50x magnification) and 100 nematodes (five replicates for the SO transect lacked enough individuals) were picked out. The individuals were transferred to glycerine (De Grisse, 1969), mounted on glass slides, and identified up to genus level and up to species level for the genus *Acantholaimus* (Guilini et al., 2016; Miljutin and Miljutina, 2016b). In addition, distribution maps of the *Acantholaimus* species found in this study and in previous literature were created. Together with the geographical range, bathymetrical ranges, based on the new and previously published records, as well as line drawings of described and undescribed species of *Acantholaimus* from this study were also provided.

Table 1
Sampling details for the ANT-XVIII/3 and SO 237 campaigns. PF (Polar Front), E MAR (East Mid-Atlantic Ridge), MAR (Mid-Atlantic Ridge), W MAR (West Mid-Atlantic Ridge). Replicates numbers represent the amount of cores used for nematode community analyses and * represent the cores used for environmental analyses.

Station	Deployment (Replicates)	Date (d/m/y)	Depth (m)	Latitude	Longitude	Remarks
SG	175-6*	4/03/2012	4155.2	50°46.59'S	39°25.33'W	South Georgia
SG	175-7*	4/03/2012	4154.2	50°46.60'S	39°25.38'W	South Georgia
SG	175-8	4/03/2012	4154	50°46.60'S	39°25.39'W	South Georgia
SG	175-9	4/03/2012	4152.1	50°46.57'S	39°25.33'W	South Georgia
HC_AEP	141-6*	18/02/2012	4113	51°15.98'S	12°37.04'W	PF(After Eddy Pump)
HC_AEP	141-9*	18/02/2012	4114	51°16.03'S	12°37.06'W	PF(After Eddy Pump)
HC_AEP	141-10	19/02/2012	4113	51°15.97'S	12°36.94'W	PF(After Eddy Pump)
HC_AEP	141-11	19/02/2012	4113.2	51°16.02'S	12°37.12'W	PF(After Eddy Pump)
HC_BEP	086-26*	1/02/2012	3966.2	51°58.87'S	12°3.76'W	PF(Before Eddy Pump)
HC_BEP	086-28*	1/02/2012	3968	51°58.74'S	12°2.11'W	PF(Before Eddy Pump)
HC_BEP	086-29	1/02/2012	3970.8	51°58.78'S	12°1.95'W	PF(Before Eddy Pump)
HC_BEP	086-30	2/02/2012	3965.4	51°58.91'S	12°2.16'W	PF(Before Eddy Pump)
LC	081-8*	19/01/2012	3760.5	51°59.99'S	9°59.99'E	PF(Low Chlorophyll)
LC	081-9*	19/01/2012	3760.7	52°0.01'S	10°0.05'E	PF(Low Chlorophyll)
LC	081-12*	19/01/2012	3757.5	51°59.93'S	10°0.06'E	PF(Low Chlorophyll)
LC	081-13	19/01/2012	3760.5	52°0.042'S	9°59.90'E	PF(Low Chlorophyll)
A1	3-3*	19/12/2014	5498	10°43.112'N	25°3.886' W	E MAR
A1	3–4*	19/12/2014	5507	10°43.108'N	25°3.888' W	E MAR
A1	3–5*	19/12/2014	5508	10°43.17'N	25°3.88' W	E MAR
A2	4-3*	25/12/2014	5771.7	10°25.11'N	31°4.61' W	E MAR
A2	4-4*	26/12/2014	5759.7	10°25.12'N	31°4.62' W	E MAR
A2	4–5*	26/12/2014	5767.7	10°25.12'N	31°4.62' W	E MAR
A3	6-2*	1/01/2015	5137	10°21.03'N	36°57.59'W	E MAR
A3	6-3*	2/01/2015	5137.4	10°21.03'N	36°57.61'W	E MAR
A3	6-4*	2/01/2015	5136.1	10°21.03'N	36°57.61'W	E MAR
A4	8-1*	6/01/2015	5182.2	10°43.562'N	42°41.593'W	MAR
A4	8–10*	8/01/2015	5117	10°42.58'N	42°40.99'W	MAR
A4	8–11*	8/01/2015	5121.9	10°42.59'N	42°40.99'W	MAR
B1	9-3*	11/01/2015	4999	11°41.37'N	47°57.36'W	W MAR
B1	9-4*	12/01/2015	4998.3	11°41.36'N	47°57.34'W	W MAR
B2	11-5*	14/01/2015	5090.7	12°5.40'N	50°26.98'W	W MAR
B2	11-6*	15/01/2015	5091.5	12°5.42'N	50°26.98'W	W MAR
B2	11-7*	15/01/2015	5091.4	12°5.40'N	50'26.97'W	W MAR

2.4. Data analyses

In order to investigate the first paradigm of biodiversity in our study (the deep sea is diverse at a local scale but turnover is limited), genus and species density and diversity were estimated. Diversity was estimated based on Shannon-Wiener diversity (H'), and genus and species richness (S). Multispatial scale variability was measured at four different levels. Using the additive partitioning approach, total nematode diversity (gamma diversity) was calculated as the sum of alpha diversity within each core (α), beta diversity within a station (β1), and beta diversity between stations from the same transect (β2) using the software PARTITION 3.0 (Crist et al., 2003). Comparisons within each hierarchical level together with differences between transects (SO and NA) were also performed. For within-level comparison, alpha diversity was calculated based on S and H', and beta diversity was obtained based on the dissimilarities within and between stations using SIMPER ((dis)similarity percentages) routines in PRIMER v6 software (Clarke and Gorley, 2006). Finally, SIMPER was also used to assess the average percent contribution of each genus/species to the total dissimilarity between stations (Anderson et al., 2007).

The nematode genus structure and *Acantholaimus* species multivariate matrix analyses were based on Bray-Curtis similarities (and Euclidean distances for the univariate data: density, S, and H'). Genus rarefaction curves were calculated based on the Chao1 estimator, which takes into account abundance values. Species matrices were used to investigate differences between regions and stations within the same regions. Non-parametric multivariate ANOVA (PERMANOVA) was used and analyses were performed using a 2-factor nested design: it included 'Region' (NA and SO) as a fixed factor and 'station' as a fixed factor nested in 'Region' (Anderson et al., 2007). Pair-wise comparisons were performed using pseudo-*t* tests obtained from the PERMANOVA permutations, and calculated as the square root of Pseudo-F. Furthermore, PERMDISP routines were used to test the homogeneity of multivariate dispersions between stations.

The data analyses for the second and third paradigm testing were interlinked through correlation and DistLM (distance-based linear model) analyses. Univariate correlations between nematode variables (density per 10 cm², S, and H') and trends in environmental variables (% TOC, % TN, % TOM, CPE, depth, NPP, and SED) were investigated using Spearman rank correlations and Draftsman plots (Anderson et al., 2007; R Core Team, 2013).

The relationship between community/species diversity/density and environmental data were performed through DistLM routines in PRIMER (Anderson et al., 2007) and used variables with correlations lower than 0.9. The environmental data was first normalized (subtracted mean divided by standard deviation) and resemblance matrices were obtained using Euclidean distances. Then, PERMANOVA tests were conducted using the same design used for species analyses (see above). Highly correlated variables were first transformed to cosine to reduce the linearity of the correlation, and if correlations persisted they were excluded from the DistLM analyses. The DistLM procedure was built using a step-wise selection and R^2 as selection criterion. Significant results for all analyses were considered when $p < 0.05$.

3. Results

3.1. Local and regional genus diversity and density compared within and between latitudinal transects

Total nematode densities were significantly higher at the SO transect in comparison with those along the NA transect (PERMANOVA $p < 0.05$). The highest values were observed at SG (235.4 ± 70 ind/10 cm²) and HC_AEP (172.8 ± 38 ind/10 cm²), which differed significantly from the other SO stations (Fig. 2a; Table S1).

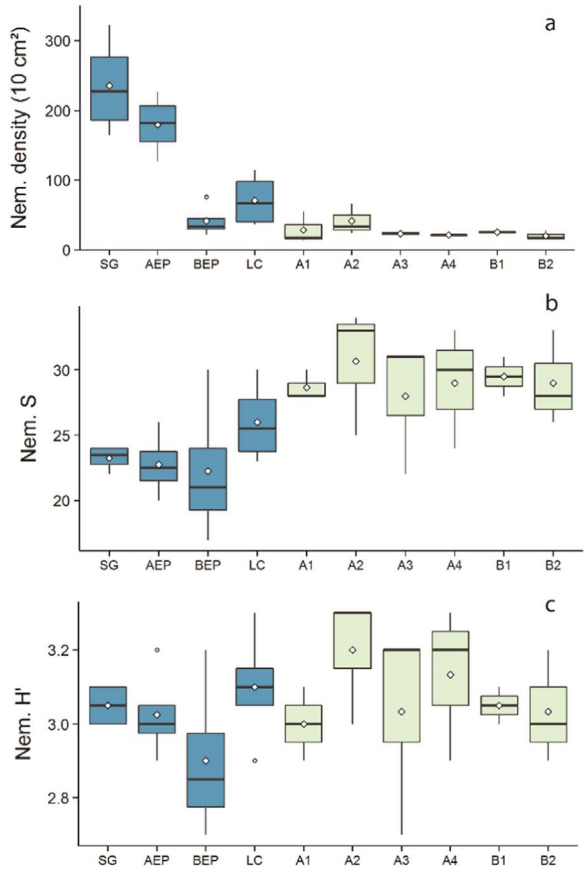

Fig. 2. Univariate nematode boxplots data for (a) total density (ind/10 cm²), (b) genus richness (S), and (c) Shannon-Wiener (H') diversity. Blue boxplots represent Southern Ocean stations and green boxplots represent North Atlantic stations. Black lines represent the median, empty circles represent the mean, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Along the NA transect, lowest densities were observed at A3 (23.3 ± 2 ind/10 cm²), although pairwise differences between NA stations were not statistically significant (Table S1).

A total of 150 nematode genera were found for the two regions. At the SO, 62 genera occurred only at this region, while 47 genera were restricted to the NA transect. The genera restricted to only one transect were mostly rare genera (< 2%) or singletons. Rare taxa ranged from 41 to 53% in the SO transect, while at the NA transect they composed from 26 to 33% of the total nematode assemblage. Average genus richness per station was significantly higher at the NA transect when compared to the SO (Fig. 2b). Pair-wise comparisons revealed no significant differences between stations from the same transect (Table S1). The abundant genera per station, with percentages ≥2%, are represented in Table 2. Shannon-Wiener diversity (H') showed no significant differences between and within both transects (Fig. 2c; Table S1).

The results for the nematode multivariate community analyses based on nematode genera relative abundances showed significant differences between regions and stations (Table S1). Pairwise comparisons revealed that for the SO, all stations were significantly different from each other, except for the pairs [HC_AEP, LC] and [HC_BEP, LC]. Stations located at the NA did not exhibit any significant difference between pairs of stations. SIMPER routines revealed a dissimilarity of 59.8% between regions. The genera *Microlaimus, Desmodora,* and *Tricoma,* found in higher abundances at the SO, and the genera *Acantholaimus* and *Thalassomonhystera,* showing higher abundances in the NA, contributed the most to the dissimilarity between regions.

Fig. 3a illustrates that dissimilarity increases with increasing geographical distance. When comparisons were performed within each transect, dissimilarities varied from 49–62% for the SO transect, and from 38–53% for the NA transect, revealing that NA stations differ less than SO stations (Fig. 3a). The genus rarefaction curve for each station from both transects only reached an asymptote for the stations SG, HC_AEP, and HC_BEP located at the SO transect (Fig. S1).

Additive partitioning results for nematode assemblages showed the highest contribution of beta diversity between stations from the same transect (β2) to the total diversity based on H' for SO and NA. (Fig. 3b). For genus richness, a different pattern was observed, where β2 explained most of the community variability for SO, while α showed greatest contribution to the total diversity for NA (Fig. 3b). The within-station diversity (β1) was higher at the SO transect for both genus richness (26%) and H' (26%), when compared to the NA (19 and 20%, respectively) stations.

3.2. Acantholaimus *species diversity, density, and distribution*

The total density of *Acantholaimus* was significantly higher at the SO stations when compared to the NA stations. SG possessed the highest densities (34.9 ± 19.6 ind/10 cm^2), followed by HC_AEP (17.3 ± 7.7 ind/10 cm^2), although pairwise comparison for this transect was only significant between the pair [SG, HC_BEP] (Table S1). The NA transect did not show any significant pairwise difference. In addition, relative abundances of this genus revealed no significant differences, neither between regions nor between stations (Fig. 4a).

For both studied regions together, 23 species of *Acantholaimus* were identified. Nevertheless, six species were represented by only one individual and/or only by females and were excluded from the analyses. From the remaining 17 species, seven species occurred only in the NA and one species was restricted to the SO, leaving nine species shared between regions (Fig. 5). Species richness was significantly higher at the NA transect when compared to the SO (Fig. 4b). Within the NA transect, significant differences were only observed for the NA pair [A2, A3] (Table S1). Also species H' values were significantly higher at the NA stations and exhibited significantly higher values at A3 (1.97 ± 0.1) compared with the other stations of the same transect (Fig. 4c). Pairwise comparisons revealed no significant differences within the stations from the SO transect (Table S1).

PERMANOVA multivariate analysis on the *Acantholaimus* species structure matrix revealed significant differences between both regions and stations (Table S1). Pairwise comparisons for both transects showed significant differences between the SO pairs [SG, LC], and the NA pairs [A2, B1] and [A2, B2]. The most abundant species for both regions was *Acantholaimus invaginatum* (33 ± 11 ind/10 cm^2), followed by *A. maks* (9.5 ± 7 ind/10 cm^2). SIMPER exhibited 70.8% dissimilarity between regions, with differences mainly attributed to higher relative abundances of *A. invaginatum* and *A. elegans* in the SO, and *A. akvavitus* in the NA. Dissimilarities in species composition of the genus *Acantholaimus* increased with increasing geographical distances (Fig. 3c). Higher dissimilarities were observed between stations within the SO transect (41–60%) than within the NA transect (31–55%) (Fig. 3c). Additive partitioning results revealed highest contribution of beta diversity between stations (β2) to the total diversity for both genus richness and H' diversity within the SO transect (Fig. 3d). For the NA transect, α diversity showed highest contribution to the total diversity for both H' and S (Fig. 3d). The within-station diversity (β1) accounted for 25% of the total diversity at SO, while at NA a lower contribution of 16% was observed.

The global distribution of species found in this study is shown in Fig. 6. A. *iubilus* was the most widespread species, having been encountered in ten different ocean basins. It was followed by *A. maks*, found in eight different ocean basins, and *A. akvavitus*, distributed in six ocean basins. The depth distribution for each species can be found in Fig. 7. The most eurybathic species found was *A. maks* (400–

Table 2
Most abundant genera (> 2%) per station (average ± st.dev.). N refers to the number of individuals picked out for each replicate and Na to the number of *Acantholaimus* individuals found for each replicate per station.

SG	%	HC_AEP	%	HC_BEP	%	LC	%	A1	%
Tricoma	11.9 ± 3.9	*Microlaimus*	17.4 ± 6.3	*Thalassomonhystera*	12.4 ± 3.2	*Thalassomonhystera*	14.0 ± 5.2	*Thalassomonhystera*	25.5 ± 0.6
Desmodora	11.2 ± 9.1	*Thalassomonhystera*	11.5 ± 1.2	*Daptonema*	7.3 ± 2.5	*Acantholaimus*	9.3 ± 5.3	*Acantholaimus*	19.0 ± 6.4
Acantholaimus	8.4 ± 5.2	*Southerniella*	5.1 ± 4.6	*Acantholaimus*	7.2 ± 3.5	*Halalaimus*	3.9 ± 1.4	*Desmodora*	6.1 ± 0.6
Microlaimus	6.8 ± 1.4	*Acantholaimus*	4.7 ± 1.7	*Diplopeltula*	4.8 ± 2.7	*Molgolaimus*	3.5 ± 3.2	*Halalaimus*	4.8 ± 0
Thalassomonhystera	3.0 ± 2.2	*Tricoma*	3.3 ± 3.4	*Microlaimus*	4.6 ± 2.2	*Microlaimus*	3.1 ± 3.0	*Prochaetosoma*	3.8 ± 0.9
Actinonema	2.8 ± 1.7	*Diplopeltula*	2.8 ± 2.4	*Theristus*	3.7 ± 2.0	*Desmoscolex*	2.7 ± 2.4	*Tricoma*	3.5 ± 0
Halalaimus	2.0 ± 1.8	*Molgolaimus*	2.3 ± 1.1	*Tricoma*	2.8 ± 3.3	*Tricoma*	2.2 ± 0.7	*Daptonema*	3.4 ± 0.6
		XYALIDAE sp2	2.1 ± 3.0	*Desmodora*	2.8 ± 2.0	*Daptonema*	2.1 ± 0.4	*Manganonema*	3.3 ± 0.6
				Enchonema	2.5 ± 1.3			*Ceramonema*	2.5 ± 1.8
				(Pareu)Desmoscolex	2.5 ± 2.3			*Southerniella*	2.5 ± 0
				Leptolaimus	2.0 ± 1.2			*Desmoscolex*	2.3 ± 1.0
N1;N2;N3;N4	99; 97; 98; 108	N1;N2;N3;N4	95; 88; 85; 97	N1;N2;N3; N4	99; 59; 47; 91	N1;N2;N3; N4	66; 89; 95; 75	N1;N2;N3	96; 99; 100
Na1;Na2;Na3;Na4	12; 20; 13; 3	Na1;Na2;Na3;Na4	5; 6; 1; 7	Na1;Na2;Na3; Na4	12; 3; 1; 13	Na1;Na2;Na3; Na4	6; 15; 13; 4	Na1;Na2;Na3	14; 23; 14
A2	%	A3	%	A4	%	B1	%	B2	%
Acantholaimus	18.3 ± 4.4	*Acantholaimus*	30.4 ± 8.6	*Acantholaimus*	25.9 ± 4.8	*Acantholaimus*	25.4 ± 14.3	*Acantholaimus*	28.5 ± 13.0
Thalassomonhystera	14.0 ± 0.56	*Thalassomonhystera*	16.8 ± 0.6	*Thalassomonhystera*	12.4 ± 0	*Thalassomonhystera*	14.3 ± 0.7	*Thalassomonhystera*	12.4 ± 0
Ceramonema	6.0 ± 3.7	*Syringolaimus*	3.8 ± 1.6	*Halalaimus*	5.8 ± 0	*Diplopeltoides*	11.1 ± 0	*Halalaimus*	5.3 ± 0
Halalaimus	5.8 ± 0	*Tricoma*	3.5 ± 0	*Pararaeolaimus*	4.7 ± 1.2	*Syringolaimus*	7.2 ± 2.2	*Cervonema*	4.5 ± 0.6
Daptonema	5.1 ± 0.1	*Daptonema*	3.5 ± 0.6	*Desmoscolex*	3.7 ± 1.2	*Manganonema*	3.6 ± 0	*Pararaeolaimus*	3.5 ± 1.6
Theristus	3.4 ± 0.6	*Desmoscolex*	3.4 ± 1.0	*Manganonema*	3.4 ± 0.6	*Halalaimus*	3.5 ± 0.7	*Syringolaimus*	3.3 ± 2.6
Paramonohystera	3.2 ± 1.8	*Halalaimus*	3.4 ± 0	*Tricoma*	3.2 ± 0	*Cervonema*	3.0 ± 1.4	*Manganonema*	3.2 ± 0.6
Actinonema	3.1 ± 2.6	*Cervonema*	3.1 ± 0	*Chromadora*	2.4 ± 0	*Pararaeolaimus*	2.6 ± 1.4	*Diplopeltula*	3.1 ± 0
Metasphaerolaimus	3.0 ± 1.2	*Manganonema*	3.0 ± 0.6	*Paramonohystera*	2.3 ± 1.0	*Tricoma*	2.6 ± 0	*Desmoscolex*	2.7 ± 0.6
Pselionema	2.8 ± 0			*Prototricoma*	2.3 ± 0	*Chromadora*	2.0 ± 0	*Daptonema*	2.3 ± 0.6
Amphimonhystrella	2.1 ± 1.2			*Ceramonema*	2.0 ± 0			*Tricoma*	2.3 ± 0
Tricoma	2.1 ± 0.6								
N1;N2;N3	101; 100; 103	N1;N2;N3	99; 100; 100	N1;N2;N3	100; 100; 100	N1;N2	100; 100	N1;N2;N3	100; 99; 99
Na1;Na2;Na3	7; 21; 14	Na1;Na2;Na3	20; 37; 30	Na1;Na2;Na3	19; 25; 27	Na1;Na2	33; 15	Na1;Na2;Na3	30; 11; 33

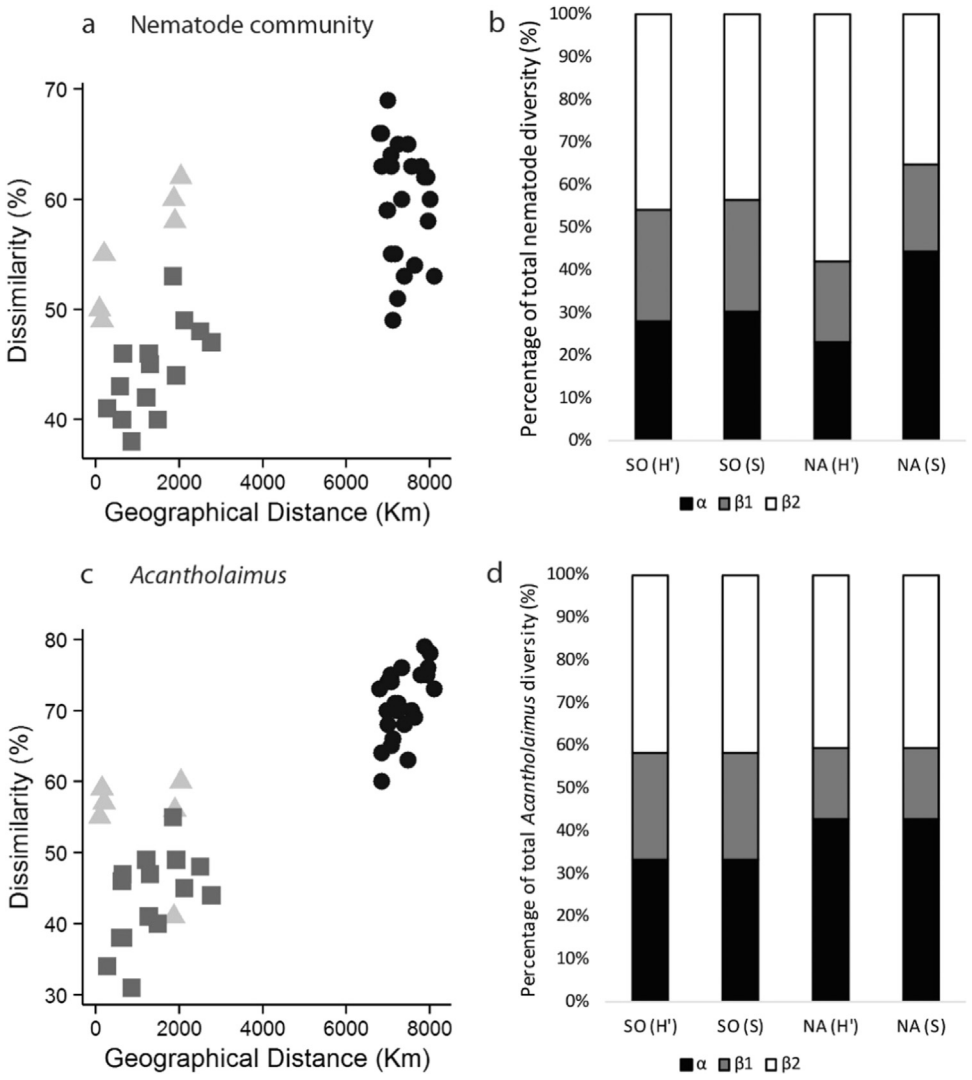

Fig. 3. Dissimilarities between nematode community (a) and *Acantholaimus* species (c) in relation to geographical distance (Km). Black circles represent dissimilarities between regions, grey triangles stand for dissimilarities between SO stations, and dark grey squares exhibit dissimilarities between NA stations. Stacked columns (b and d) represent the additive partitioning per transect (Southern Ocean (SO) and North Atlantic (NA)) of species richness (S) and the Shannon index of diversity across three sampling scales: α=within each core, β1=within stations, and β2=between stations from the same transect.

6313 m), followed by *A. mirabilis* (34–5767 m), *A. megamphis* (160–5508 m), and *A. invaginatum* (511–5771 m). Sp6 was the only species restricted to a single depth range. Nine species were only encountered in abyssal plains (Fig. 7).

3.3. Benthic-pelagic coupling and patch-mosaic dynamics

3.3.1. Environmental variables

Mean values for abiotic variables are shown in Fig. 8. Sediment diversity (SED) revealed significant differences between regions (Table 3). SED significantly decreased eastwards for the SO stations due to the increase in silt-clay content, while for the NA stations a significant westward increase (except for station A1) was observed (Fig. 8a). Highest SED were observed at stations B1 and B2 (1.0 and 0.68, respectively). The main differences between stations were derived from the greater content of very fine sand, fine sand, and medium sand at the stations with higher SED. Pairwise comparisons between stations for each region can be found in Table 3. In addition, total organic matter content (% TOM) showed significant differences between regions, and between stations within the same transects (Fig. 8b). Significant pairwise comparisons for SO and NA can be found in Table 3. Total organic carbon content (% TOC) was significantly higher at SO (from 0.77 to 1.14%) (Fig. 8c), while pairwise comparisons within transects revealed significant differences only between NA stations (Table 3). Total nitrogen (% TN) (Fig. 8d) average values did not differ significantly, neither between regions nor between stations.

Chloroplastic pigment equivalents (CPE) were significantly higher at the SO transect (Fig. 8e). Higher mean values were observed at the SG station (22.5 ± 16.5 μg/g), although those were highly variable between replicates and not significantly different from other stations. Low CPE content was observed for all other stations and, although significant differences were found between regions and stations ($p < 0.05$) in the PERMANOVA analyses, no significant differences were observed between pairs of stations within transects (Table 3). Net primary productivity values (NPP) revealed no significant differences between regions, but significant differences appeared between stations located at the SO transect (Table 3). NPP were significantly higher at SG station (539 ± 0 g C/m² month) and decreased eastwards for the SO stations (Fig. 8f). For the NA stations, NPP slightly decreased westwards, but pairwise comparisons were not significant. Yearly NPP trends showed a higher variation between months at the SO region than at the NA transect (Fig. 9), revealing a higher seasonality at the first transect.

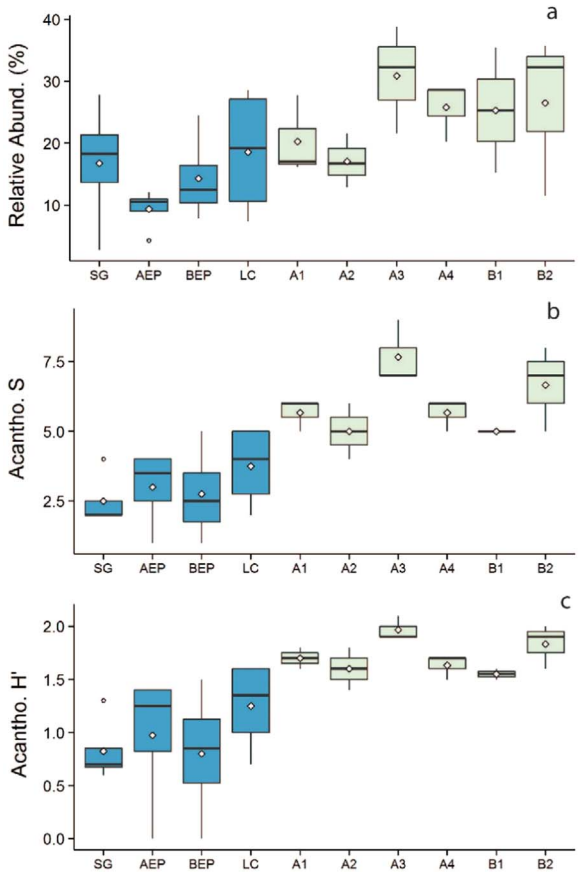

Fig. 4. Univariate boxplots data for *Acantholaimus* (a) relative abundance (%), (b) species richness (S), and (c) Shannon-Wiener diversity (H'). Blue boxplots represent Southern Ocean stations and green boxplots represent North Atlantic stations. Black lines represent the median, empty circles represent the mean, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3.2. Correlation between environmental variables with nematode genera and Acantholaimus *species relative abundance and biodiversity*

Univariate correlations between nematode response variables (nematode total density, richness, H', and *Acantholaimus* density, relative abundance, and richness) and environmental predictor variables (CPE, % TN, % TOC, % TOM, NPP, and SED) revealed no significant results.

DistLM routines based on the nematode community structure for seven environmental variables explained 24% of the total community variation (Table S3). The values of % TOC and CPE displayed a significant impact on the nematode relative abundance, whereas the other variables did not contribute significantly to the model.

The DistLM analysis of the *Acantholaimus* species structure revealed a significant effect of % TOC, CPE, NPP, and % TOM on the differences between species, accounting together for 40% of the total variation (Table S3). The other environmental variables used for the model did not exhibit a significant correlation on the fitted model.

4. Discussion

4.1. The deep sea is diverse at a local scale, while turnover can be restricted

Nematode genus and *Acantholaimus* species alpha diversity (i.e. local species richness and Shannon-Wiener diversity of individual cores) was similar to other studies conducted in abyssal plains. However, caution should be exercised when comparing results, as different sampling equipment and sediment layers were used, hampering exact comparisons of diversity at a macro scale between different areas (compare Miljutina et al., 2010; Muthumbi and Vincx, 1997; Sebastian et al., 2007; Singh et al., 2014; Thistle et al., 1985; Vanreusel et al., 2010). In this study, the North Atlantic (NA) transect showed higher alpha genus and *Acantholaimus* species diversity and richness per sample when compared to the local (i.e. alpha) diversity in the Southern Ocean (SO) transect. One has to take into account that the sampling cores used at the NA stations sampled a larger surface (25.5 cm² for SO vs. 69.4 cm² for NA), which could result in the higher diversity found there. Nevertheless, the same number of nematodes was picked out randomly after sample homogenisation in order to allow between-sample comparisons, and rarefaction curves did reach an asymptote for the SO stations (except for LC), partially eliminating sampling biases related to the sample size.

Despite the higher local diversity exhibited at the NA transect when compared with the SO transect, abyssal plains can generally be distinguished by a set of dominant taxa, such as the nematode genera *Acantholaimus* and *Thalassomonhystera* (Vanreusel et al., 2010). In this study, these two genera were also dominant at every station of the NA transect and at the LC station in the SO. Also the same *Acantholaimus* species were shared between both areas. These results

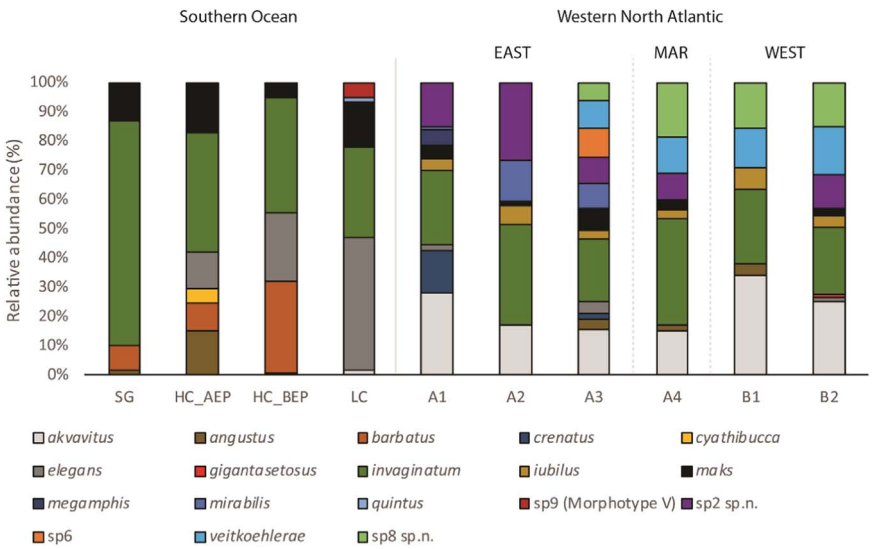

Fig. 5. Relative abundances of *Acantholaimus* species per station for each transect. MAR=Mid-Atlantic Ridge.

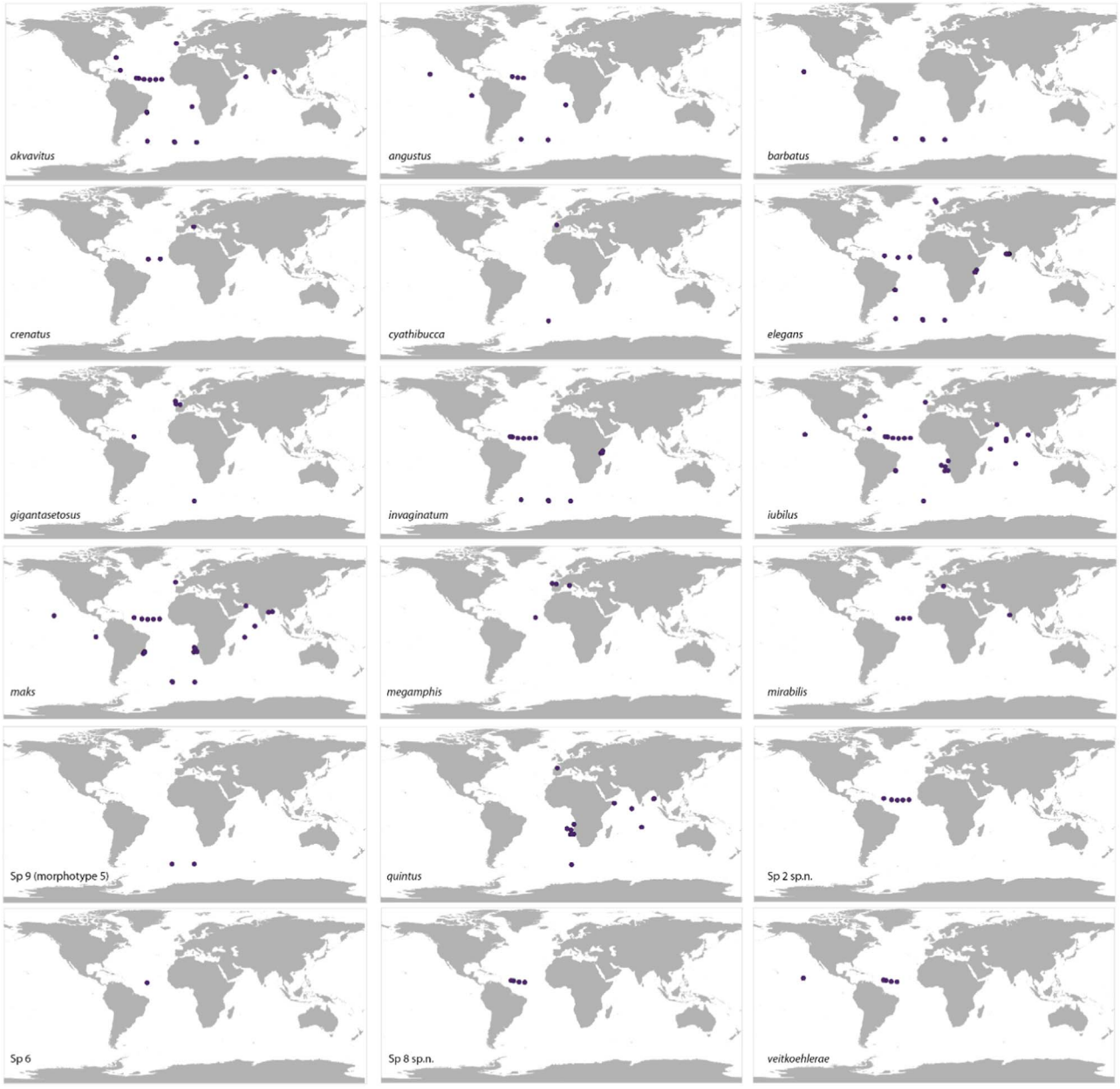

Fig. 6. Species occurrences for *Acantholaimus* species found in this study combined with records from the literature (Table S2).

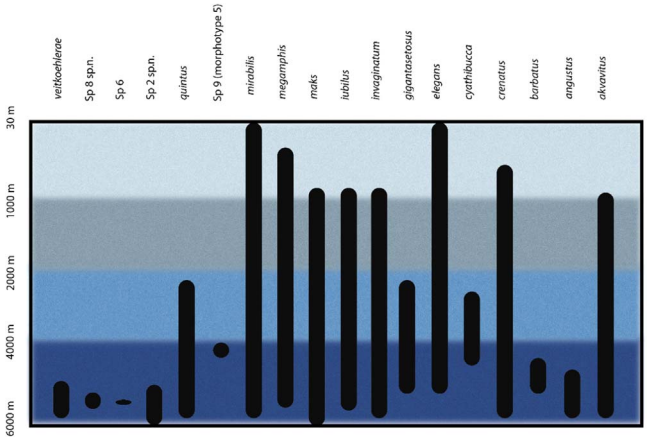

Fig. 7. Depth distribution of the *Acantholaimus* species found in this study combined with previous records from the literature (Table S2). Sp 9 in this study is referred as morphotype 5 by Lins et al. (2015).

confirm the homogeneous nature of abyssal sediments on an large scale and suggest that for these deep areas "everything is everywhere, but the environment selects" at the genus and species levels, when environmental conditions are favourable (Baas-Becking, 1934; Fenchel and Finlay, 2004; Moens et al., 2014). Thus, although genus and *Acantholaimus* species local diversity was higher at the NA transect when compared to the SO, overall the same abundant nematode taxa were found, revealing a low turnover between NA stations. Nevertheless, the distribution of species in the deep sea could be better supported with further molecular analysis, since the species reported here could also represent cryptic species. A previous study has already suggested low endemism for nematodes in the deep sea (Bik et al., 2010), but whether this pattern is taxon specific is still not clear.

This observed high local diversity and dominance of specific nematode genera was already expected based on previous studies (Lambshead, 2004; Lambshead and Boucher, 2003), confirming thus, that the deep sea is diverse at a local scale. Nevertheless, the expected low beta diversity already reported for nematodes (Fenchel and Finlay,

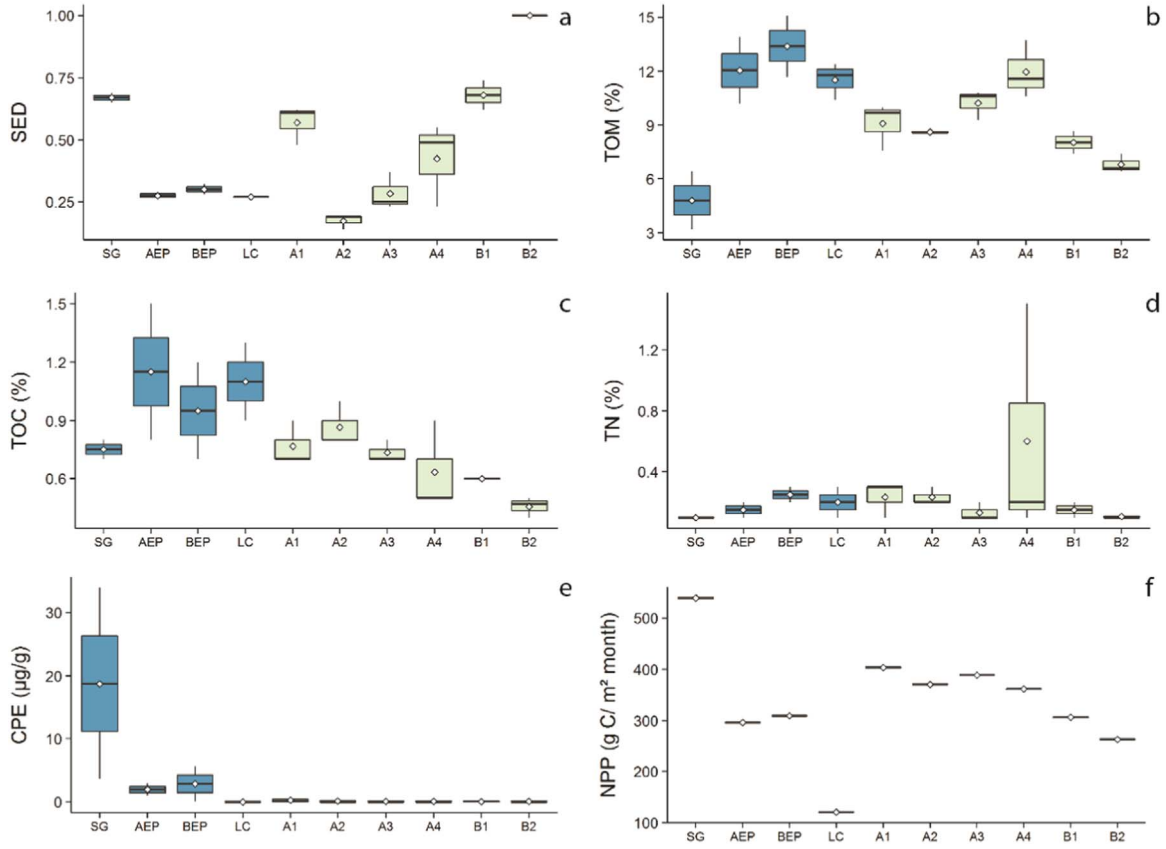

Fig. 8. Environmental variables used in this study per station: (a) SED (sediment grain size diversity), (b) TOM (Total Organic Matter), (c) TOC (Total Organic Carbon), (d) TN (Total Nitrogen), (e) CPE (Chloroplastic Pigment Equivalents), (f) NPP (average Net Primary Productivity). Blue boxplots represent Southern Ocean stations and green boxplots represent North Atlantic stations. Black lines represent the median, empty circles represent the mean, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2004; Lambshead, 2004; Leduc et al., 2012a) could not be confirmed here for both studied transects. When dissimilarities in nematode genus and *Acantholaimus* species structure were compared between stations from the same transect (β2), beta diversity for genera and species was higher for the SO transect than for the NA (Fig. 3a and c), indicating that turnover was greater in the first. In addition, the additive partitioning results revealed differences between both transects regarding the contribution of local and regional diversity to the total genus and species variability (Fig. 3b). For genus richness, alpha diversity accounted for most of the total diversity at the NA transect, while beta diversity between stations (β2) was proportionally much higher for genus H'. The higher importance of turnover (β2) when H' was considered is probably due to the dominance of *Acantholaimus* (up to 30%) within the NA stations, since H' takes both abundance and evenness into consideration. The highest contribution of β2 for both genus richness and H' was revealed in the SO, and this higher turnover

Table 3
PERMANOVA results for the environmental variables used in this study. SED (sediment grain size diversity), TOM (Total Organic Matter), TOC (Total Organic Carbon), TN (Total Nitrogen), CPE (Chloroplastic Pigment Equivalents), NPP (average Net Primary Productivity). Main *p* perm represents p-values for the 2-factor nested design test. Significantly different p-values are displayed in bold. Pairwise *t*-test results are only shown if values were significant. When all differences between stations pairs were not significant, pairwise *t*-tests were displayed as ND.

Abiotic variable	Main test *p* perm	pairwise t-tests for SO		pairwise *t*-tests for NA			
SED	Region=***0.0005***	SG, HC_AEP	***0.032***	A1, A2	***0.0009***	A3, B1	***0.0145***
	Site=***0.0001***	SG, HC_BEP	***0.0059***	A1, A3	***0.0092***	A3, B2	***0.0002***
		SG, LC	***0.0001***	A1, B2	***0.0006***	A4, B2	***0.0035***
				A2, B1	***0.0016***	B1, B2	***0.006***
				A2, B2	***0.0001***		
% TOM	Region=***0.0357***	SG, LC	***0.0196***	A2, A3	***0.0278***	A3, B2	***0.0035***
	Site=***0.0001***			A2, A4	***0.0226***	A4, B2	***0.0072***
				A2, B2	***0.0043***		
% TOC	Region=***0.027***	ND		A1, B2	***0.0117***	A3, B2	***0.0012***
	Site=0.2067			A2, B2	***0.0089***	B1, B2	***0.0354***
% TN	Region=0.7135	ND		ND			
	Site=0.5817						
CPE	Region=***0.016***	ND		ND			
	Site=***0.0263***						
NPP	Region=***0.0001***	SG, HC_BEP	***0.0002***	ND			
	Site=***0.0001***	HC_AEP, HC_BEP	***0.0094***				
		HC_BEP, LC	***0.0001***				

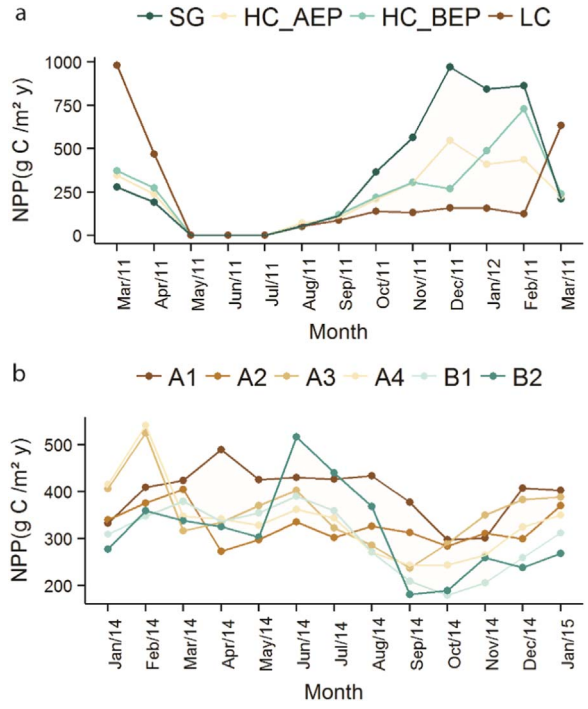

Fig. 9. Values of net primary productivity (NPP) per month for the SO (a) and NA (b) stations during the years 2011/2012 and 2014/2015, respectively.

might be explained by the higher aggregation of organisms and by the high number of rare genera (62 genera were restricted to this region) found in this transect (Gering and Crist, 2002), and not by the core size, since SO rarefaction curves reached an asymptote (except for LC). Nematode community structure in the SO was not only different between stations, but also diverged in terms of community structure from the usual communities found in other abyssal areas (Lambshead et al., 2003; Miljutina et al., 2010; Singh et al., 2014; Vanreusel et al., 2010). However, the question remains if environmental differences rather than geographical distances are responsible for the high turnover between these stations (see below).

Additive partitioning results for the *Acantholaimus* species revealed contrasting patterns for the SO and NA transects (Fig. 3d). While turnover between stations (β2) contributed most to total *Acantholaimus* (species richness and H') species diversity between stations along the SO transect, alpha diversity contributed the most for species divergences (species richness and H') in the NA. Therefore, the SO transect did not follow the expected high local, low regional diversity previously reported for nematode distribution. These results do not support the second part of the paradigm about limited species turnover in the deep sea (Lambshead and Boucher, 2003).

Our results indicate more divergent communities at a regional scale along the Polar Front than across the NA transect, where a more homogenous genus pool seems to be present covering the whole NA study area, since none of the stations differed significantly in genus structure. This may seem a remarkable observation for organisms lacking a pelagic life stage, as the NA transect was ~1500 km long and interrupted by the Mid-Atlantic Ridge, but similar wide distributions were already reported for deep-sea nematodes, suggesting low endemism of this group (Bik et al., 2010; Zeppilli et al., 2011).

At species level, a high degree of cosmopolitanism was observed for many species of *Acantholaimus* (Fig. 10). Two species, *A. invaginatum* and *A. maks* were encountered at all stations (except station B1 for *A. maks*) of this study, having been also previously observed in different ocean basins (Table S2). Global literature-based distribution maps of *Acantholaimus* species showed that *A. invaginatum* and *A. maks* (together with *A. megamphis* and *A.mirabilis*) are also the ones covering a larger bathymetrical range, occurring from the continental shelf to the abyss (Fig. 7). These results are unexpected since bathymetry is considered an ecological barrier for many taxa, limiting species dispersal in the deep sea (Etter et al., 2005; Etter and Bower, 2015; Havermans et al., 2013; Wilson, 1983). However, molecular evidence would be required to identify haplotype distribution for these eurybathic morphospecies assisting in the inference of connectivity or divergence. The number of *Acantholaimus* species found in this study was similar to other studies (Muthumbi and Vincx, 1997; Thistle et al., 1985) except for the high number of morphotypes found by De Mesel et al. (2006) along the Antarctic continental shelf and slope. The success of *Acantholaimus* on the Antarctic shelf is not in accordance with its establishment in the oligotrophic abyss and requires further investigation.

The idea of the deep sea (> 1000 m) as a highly diverse environment (Hessler and Sanders, 1967), possessing greater richness at a local scale compared to shallower environments (Gage, 1996), should be interpreted with caution. We have observed in this study that the comparison of diversity can depend on the area studied, on the spatial scale used, and on the choice of the diversity index. The high diversity at local scale (alpha diversity) accounted for the deep sea, thus, cannot be considered a general rule for all environments. For genus richness, for e.g., high beta diversity can be derived from the high number of rare taxa, but undersampling and poor taxonomic identification may be partly responsible for their high turnover. Therefore, macro-scale trends of benthic deep-sea diversity still remain largely unknown, being based on local and regional descriptions (Gooday et al., 2004; Woolley et al., 2016).

In general, our results corroborate the idea that deep-sea environments provide relatively few barriers to dispersal (Grassle, 1989; van der Heijden et al., 2012), enabling connectivity between extensive areas, and consequently low endemism, particularly for nematodes (Bik et al., 2010; Strugnell et al., 2008; van der Heijden et al., 2012). The wide distribution of many nematode genera and *Acantholaimus* species in this study suggests either that radiation of nematodes in abyssal environments occurred a long time ago, or that dispersal of nematodes is highly efficient, promoting a widespread distribution of individuals (Bik et al., 2010; Tietjen, 1989; Zeppilli et al., 2011). Concurrently, the different nematode community observed for SG, HC_AEP, and HC_BEP in this study, and the high levels of endemism that has been reported for some shallow-water nematode taxa (Derycke et al., 2013; Van Campenhout et al., 2014) also suggest that habitat type and environmental conditions might play a role in shaping nematode assemblages or specific nematode taxa, and consequently nematode distribution (Heip et al., 1985; Moens et al., 2014; Vincx et al., 1994).

4.2. Deep-sea diversity does not increase with increasing organic matter input at a local scale

Although no correlation was observed between univariate data for the total nematode genus and *Acantholaimus* species assemblages (density and diversity) and organic matter input, DistLM results based on the multivariate community data reflected a significant effect of % TOC, CPE, and NPP on the nematode genus and *Acantholaimus* species structure. Highest densities of nematodes were observed at the SG station, characterized by the highest average net primary productivity (NPP). In general, marine nematode densities are highly correlated with food input in the sediments (Lambshead, 2004), and here highest total densities were observed at the SO transect. The increasing densities of benthic organisms with increasing food input in abyssal plains has been documented repeatedly for meiofaunal and macrofaunal groups (Danovaro et al., 2013; Gage et al., 2004; Glover et al., 2001; Gooday and Jorissen, 2012). In contrast, nematode genera and *Acantholaimus* species diversity differed for both studied transects. The highest contribution of alpha diversity was found at the NA

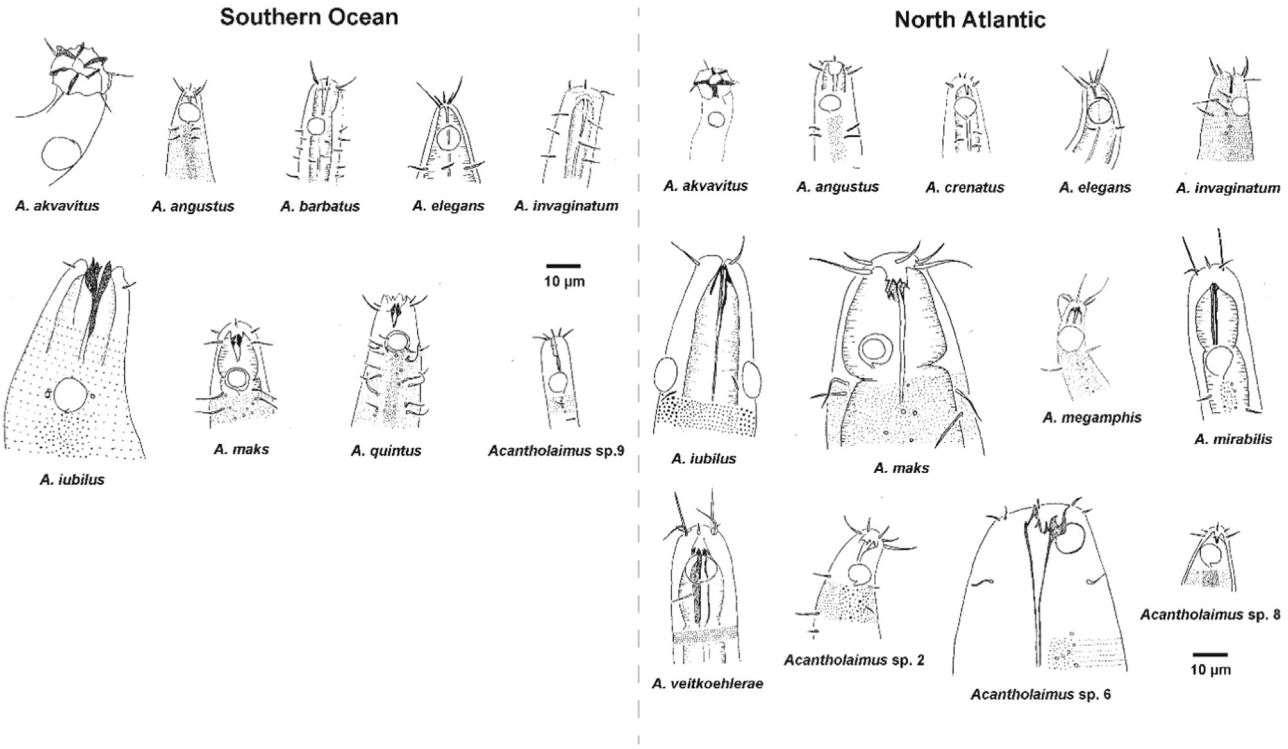

Fig. 10. Line drawings of the *Acantholaimus* species found at the Southern Ocean and the North Atlantic transects. Only species for which male specimens were found are presented.

transect, while turnover was more pronounced at the SO transect.

The low turnover observed for the NA, the high turnover reported for the SO, and the lowest genus and species diversity exhibited at the SG station are in accordance with the species-energy hypothesis, where the effect of organic matter input on the diversity is believed to be expressed as a parabolic curve (Leduc et al., 2012b; Whittaker et al., 2001). In this hypothesis, the amount of available energy, here understood as food availability, sets limits to the richness of the system, where both extremes (very low and high food availability) can diminish local diversity (Leduc et al., 2012b; Moens et al., 2014). In this regard, the general relative stability of the deep-sea abyssal plains under low food input, when compared to other environments, is believed to promote local diversity by reducing rates of interactions between organisms and enhancing the evolution of specialized forms (Snelgrove and Smith, 2002). This could explain the higher nematode and *Acantholaimus* species alpha diversity found at the NA transect, which is characterized by annual low and constant food input (Jochem and Zeitzschel, 1993; Longhurst, 1998). The genus *Acantholaimus* is typically abundant in abyssal plains and tends to increase in importance (relative abundance) and diversity with increasing water depth (Muthumbi and Vincx, 1997; Soetaert and Heip, 1995). In addition, this genus exhibits high inter-specific buccal parts variability, as shown in Fig. 10, indicating food selectivity as a potential strategy for species coexistence in food-depleted environments representing exclusive adaptations to certain food sources.

Therefore, the high local diversity and low turnover observed at the NA can be explained by a potential stability of this transect, which is characterized by a constantly low food input. However, low organic matter input also seems to be responsible for the homogeneous pattern of nematode community structure that is generally found in abyssal plains, supporting the “everything is everywhere, but the environment selects” hypothesis (Baas-Becking, 1934; Fenchel and Finlay, 2004; Vanreusel et al., 2010). In contrast to this low turnover and common abyssal community found at the NA transect, we have observed in our study that the stations SG, HC_AEP, and HC_BEP possessed higher turnover rates and divergent nematode genera and *Acantholaimus* species structure when compared to other studies (Miljutina et al., 2010; Singh et al., 2014). In general, higher beta diversity can be observed in environments subjected to pulsed food input, which is responsible for increasing patchiness, and consequently diversity, which can be unevenly distributed (Lambshead, 2004). This idea of relating diversity to aggregation was proposed by Shorrocks and Sevenster (1995), and our results for the SO corroborate their idea of species coexistence in patches. They stated that, if communities are patch-dependent, then within-habitat variability would be lower and among-habitat diversity would be higher than expected (Shorrocks and Sevenster, 1995) (Fig. 3).

Furthermore, pulsed organic matter input regimes can promote the dominance of opportunistic species (Grassle, 1989; Levin et al., 2001; Whittaker et al., 2001). The genus *Microlaimus*, which occurred in high abundances at HC_AEP and HC_BEP, as well as at SG may indicate an opportunistic behaviour in response to food input at these sites respectively. This genus has been reported from other bathyal and abyssal areas of the Southern Ocean and elsewhere, and when present in high abundances, this has generally been correlated to either fresh food input or to disturbance events (Hauquier et al., 2016; Lee et al., 2001; Sebastian et al., 2007) suggesting an opportunistic character. Moreover, the highest surface productivity values at SG were correlated to the lowest alpha diversity values at this station for, both, nematode genera and *Acantholaimus* species. This could be a result of the increase in density of few competitive taxa, such as *Microlaimus* and *Desmodora*, at SG, in response to the high surface productivity (Gooday, 2002; Woolley et al., 2016). The genus *Desmodora* was represented by only one species, *D. profundum,* which dominated the nematode community at SG (Lins et al., 2015). This genus is normally found in food-rich environments, such as seeps, vents, and seamounts, and has also been reported from adjacent areas, but *Desmodora* was not commonly observed in high abundances in abyssal plains (Ingels et al., 2006; Vanreusel et al., 2010). As a result, the low species diversity of *Acantholaimus* would be a consequence of a stronger competition rather than a lack of response to organic matter input. Therefore, the heterogeneity in food input for the SO transect lead to a higher turnover of nematode genera/species, and consequently to a more heterogeneous environment at a regional scale.

4.3. Increased patch dynamics (does not) increase local diversity

The influence of patch-dynamics on species coexistence at a small scale (β1) can be shaped by at least three different factors: sediment composition and diversity, sediment topography, and partitioning of food resources related to particle size (Levin et al., 2001; Tyler, 1995). In order to investigate patchiness in sediment composition, variability at the β1 level (i.e. between cores from the same station) was considered. In this study, within-station sediment diversity (SED) was in general higher for NA stations than for SO stations. Contrastingly, β1 diversity exhibited similar within-station variation for both transects. In fact, differences in nematode genus diversity and species diversity of *Acantholaimus,* and differences in SED between cores from the same stations were not concurrent, meaning that community divergences could not be explained by differences in SED. Nevertheless, sediment structuring is believed to be a major factor shaping meiofaunal communities and explaining diversity in the deep sea (Grassle, 1989; Leduc et al., 2012c). Levin et al. (2001) stated that more species are able to coexist where sediment grain size is more heterogeneous. The lack of correlation between nematode diversity and SED might be due to the range which SED varied in this study. Here, SED ranged from 0.14–1.0, while in other studies it showed much higher values (Leduc et al., 2012d; Pape et al., 2013a). This indicates that, although sediment differences were present, these were not large enough to influence nematode genus and species coexistence.

However, the greater SED observed at NA is untypical for abyssal plains. Environments possessing a higher SED, specially for abyssal plains which are dominated by silt-clay sediments, are generally more dynamic (Gage, 1997). More dynamic environments can lead to an increase in roughness and habitat heterogeneity of the sea bottom, consequently increasing the presence of mounds and burrows which contribute to the accumulation and patchiness of organic matter (Gage, 1997). The Vema area has a strong influence from the eastward Antarctic Bottom Water (AABW) flux, which can exhibit bottom currents of 18–35 cm/s and increased turbidity (Eittreim et al., 1983; Ludwig and Rabinowitz, 1980; Morozov et al., 2015), enabling passive dispersal of organisms through the transform. Small organisms, such as nematodes, are easily resuspended and transported through the water column (da Fonseca-Genevois et al., 2006; Gallucci et al., 2008). Therefore, the high bottom dynamics at the NA transect might have influenced the sediment topography, and increased species distribution ranges. At the same time, if nematodes can be passively resuspended into the water column, this might also have favoured the low beta diversity (β1 and β2) observed for this transect, together with the low and constant surface primary productivity already discussed in the previous section.

5. Conclusions

Our results are partially in agreement with Paradigm 1. Although for the North Atlantic a high alpha diversity and low turnover (i.e. beta diversity) was observed, turnover might not be necessarily low in the deep sea and can be related to the environmental conditions prevailing at different areas studied. The high local alpha diversity at the North Atlantic transect, associated with a low turnover rate between stations (β2), both at genus and *Acantholaimus* species level, are probably related to the stability of this environment due to the constant and low food input usually found at abyssal plains. Nevertheless, despite the high local diversity observed at the North Atlantic transect, all of its stations were dominated by the same nematode genera (*Acantholaimus* and *Thalassomonhystera*), corroborating the hypothesis that “everything is everywhere, but the environment selects”. The different nematode communities found in the Southern Ocean in relation to other deep-sea abyssal areas, and the higher turnover of genera and species of *Acantholaimus*, indicate that turnover might be dependent on the surface productivity and seasonal input of organic matter. Increased organic matter input at some Southern Ocean stations might have resulted in a lower alpha diversity but a higher beta diversity due to a shift in dominant genera and species between stations. Thus, these results corroborate Paradigm 2, surface productivity regulates diversity. Finally, sediment heterogeneity did not significantly influenced genus or species coexistence in this study possibly due to the low sediment variability compared to other deep-sea environments. Although the NA transect possessed higher SED and higher alpha diversity, sediment variability was not related to community differences at a small (β1) scale. Therefore, based on the results of this study, Paradigm 3 could not be validated, as patchiness did not show any association with nematode community structure at a small scale.

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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.dsr2.2016.12.005.

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