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α-, β-, γ-, δ- and ε-diversity of deep-sea nematodes in canyons and open slopes of Northeast Atlantic and Mediterranean margins

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ABSTRACT: Meiofaunal biodiversity, with a special focus on nematodes, was investigated in 6 submarine canyons and 5 adjacent open slopes along bathymetric gradients (from ca. 200 to 5000 m depth) from 3 deep-sea regions (northeastern Atlantic, western and central Mediterranean) spanning >2500 km and across a wide gradient of trophic and physicochemical conditions. The analysis of local (α) diversity at equal depths showed the presence of similar values in the NE Atlantic and Mediterranean deep-sea sediments. The comparison of the α diversity between different deep-sea habitats (canyons versus adjacent open slopes) revealed the lack of significant differences in species richness in most of the investigated systems. However, the analysis of nematode species composition showed the presence of major differences among different sampling depths (i.e. 500 versus 1000 versus 2000 m depth) and habitats. Turnover (β) diversity was high in all of the investigated deep-sea systems, but was higher in the NE Atlantic (87%) than in the Mediterranean margins (range 51 to 60%), resulting in higher values of regional (γ) diversity in the Atlantic margin. Turnover diversity among regions (δ diversity) was highest (~91%) between the NE Atlantic and western Mediterranean, but still extremely high between the western and central Mediterranean margins (~80%), thus leading to similar values of biogeographical diversity (ε) in the NE Atlantic and Mediterranean deep biogeographical provinces. The results suggest that biogeographic differences in deep-sea species composition are related to differences in β and δ diversity and not to differences in α diversity, and that the analysis of the factors driving β diversity are crucial to understand the spatial patterns of biodiversity in the deep sea.

KEY WORDS: Deep-sea nematodes · Biogeography · Canyons · Open slopes · Mediterranean Sea · Atlantic Ocean

INTRODUCTION

Deep-sea sediments cover more than 65% of the Earth's surface. Research conducted in the last 2 decades has completely changed our perception of the characteristics and functioning of these ecosystems (Gage & Tyler 1991). We know now that deep-sea ecosystems can be highly complex, diverse and characterized by high spatial and temporal variability (Rex et al. 2001, 2005, Gaston 2000, Lambshead et al. 2000, Gage 2004, Danovaro et al. 2008a), but the knowledge of the factors controlling bathymetric, latitudinal and longitudinal patterns is still very poor (Snelgrove & Smith 2002, Danovaro et al. 2004, Canals et al. 2006, Danovaro et al. 2008a). Among these factors, spatial heterogeneity of the deep-sea benthic habitats can significantly influence several biological variables including local (α) and turnover (β) biodiversity.

Continental margins are extremely heterogeneous, due to their high topographic complexity, and characterized by the presence of different habitats (such as canyons, open slopes and landslides; Canals et al. 2004, Weaver et al. 2004). Deep-sea topographic heterogeneity can affect regional hydrodynamics with

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important effects on the entire food chain, from phytoplankton to marine mammals (Gage et al. 1995, Vetter & Dayton 1998, Duineveld et al. 2001). Deep-sea canyons, for instance, are important pathways for the transport of organic carbon to the ocean's interior, and fast-track corridors for material rapidly transported from the land to the deep sea (Canals et al. 2006). The peculiar topographic and hydrodynamic features of deep-sea canyons (including bottom currents, sedimentation rates and vertical fluxes) contribute to create peculiar benthic habitats (Gili et al. 1999, Yoklavich et al. 1999), which support high rates of oxygen consumption, high values of benthic faunal biomass and diversity (Greene et al. 1988, Gage & Tyler 1991, Vetter 1995, Accornero et al. 2003). Moreover, these systems display a high level of endemism, possibly linked to conditions that promote speciation (Wilson & Hessler 1987, Jablonski & Bottjer 1990).

The high values and peculiarity of the biodiversity inhabiting canyons has led to identification of these systems as hot spots of deep-sea biodiversity (de Boveé et al. 1990, Soetaert & Heip 1995, Danovaro et al. 1999, Baguley et al. 2006, Garcia et al. 2007), but comprehensive comparisons among canyons and adjacent slopes under different regional settings are scant (Garcia et al. 2007, Van Gaever et al. 2009).

Meiofauna are the numerically dominant metazoan components of the deep-sea benthos (Vincx et al. 1994). Nematodes are the most abundant metazoan meiofaunal taxon, and their dominance increases with water depth (up to >90%; Thiel 1975, Heip et al. 1985, Cook et al. 2000, Lambshead & Schalk 2001, Danovaro et al. 2002). Nematodes are ubiquitous in all deep-sea regions and are characterized by potentially high species richness (Jensen 1988, Tietjen 1992). They play an important role in the benthic trophodynamics and their feeding ecology can be inferred from the morphology of their mouth cavity (Wieser 1953, Jensen 1987, Soetaert & Heip 1995), thus offering the opportunity to examine patterns of structural and functional (trophic) diversity in the deep sea (Danovaro et al. 2008b).

In the present study, we compared meiofaunal diversity (higher taxa) and nematode species richness from 3 deep-sea regions: the northeastern Atlantic Ocean and the western and central Mediterranean basin, characterized by different topographic settings, productivity and physicochemical conditions. We also investigated bathymetric patterns of biodiversity and compared the species richness (α-diversity) and turnover in species composition (β-diversity) of deep-sea canyons and adjacent open slopes in order to identify factors controlling deep-sea biodiversity along continental margins and the role of these in promoting regional (γ) diversity.

MATERIALS AND METHODS

Sampling. Samples were collected from the northeastern Atlantic Ocean (Portuguese margin) and the western (Catalan margin) and central (South Adriatic margin) Mediterranean Sea (Fig. 1). Overall, 6 deep-sea canyons and 5 adjacent open slopes were investigated. The same sampling strategy was utilised in all regions: sediment samples were collected from 44 stations at standard water depths, along the main axis of the canyons and the adjacent open slopes at standard depth (ca. 200, 500, 1000, 2000, 3000, 4000 and 5000 m depth, depending on the highest depth of the slope in each region). In the northeastern Atlantic, sediment samples were collected in September 2006 from 21 stations (at depths ranging from 416 to 4987 m) using the RV 'Pelagia'. Two canyons (the Nazaré and Cascais) and 2 adjacent open slopes (hereafter, the N and S Portuguese slopes) were investigated. In the western Mediterranean (Catalan margin), sediment samples were collected from 12 stations (at depths ranging from 334 to 2342 m) in October 2005 using the RV 'Universitatis'. Two canyons (the Cap de Creus/Sete and Lacaze-Duthiers) and 2 adjacent open slopes (hereafter the N and S Catalan slopes) were compared. In the central Mediterranean (South Adriatic margin), sediment samples were collected in May 2006 using the RV 'Urania' from 11 stations (depths ranging from 196 to 908 m) in 2 canyons (canyons B and C) and adjacent open slope (hereafter the S Adriatic slope). In all deep-sea regions, sediment samples were collected using a multiple corer and/or a NIOZ-type box corer allowing the recovery of virtually undisturbed sediment samples. The 2 sampling devices proved to be equivalent in the sampling of sedimentary and biotic variables (Danovaro et al. 1998). At all sampling stations, 3 sediment cores (internal diameter 3.6 cm) from the independent deployments (whenever possible) were analysed for meiofaunal parameters (0 to 15 cm) and nematode diversity (0 to 1 cm). Sediment samples for organic matter analysis (the top 1 cm from 3 different cores) were preserved at –20°C until analysis in the laboratory.

Meiofaunal analyses. For meiofaunal extraction, sediment samples were sieved through 1000 µm mesh, and a 20 µm mesh was used to retain the smallest organisms. The fraction remaining on the latter sieve was resuspended and centrifuged 3 times with Ludox HS40 (density 1.31 g cm^{-3}) according to Heip et al. (1985). All meiobenthic animals were counted under a stereomicroscope and classified per higher taxon after staining with Rose Bengal (0.5 g l^{-1}). All animals except for nematodes were identified to higher taxa (sensu De Troch et al. 2006).

Nematode diversity. For nematode diversity analysis, 100 nematodes for each of the 3 replicates (or all nematodes when the abundance was lower than 100

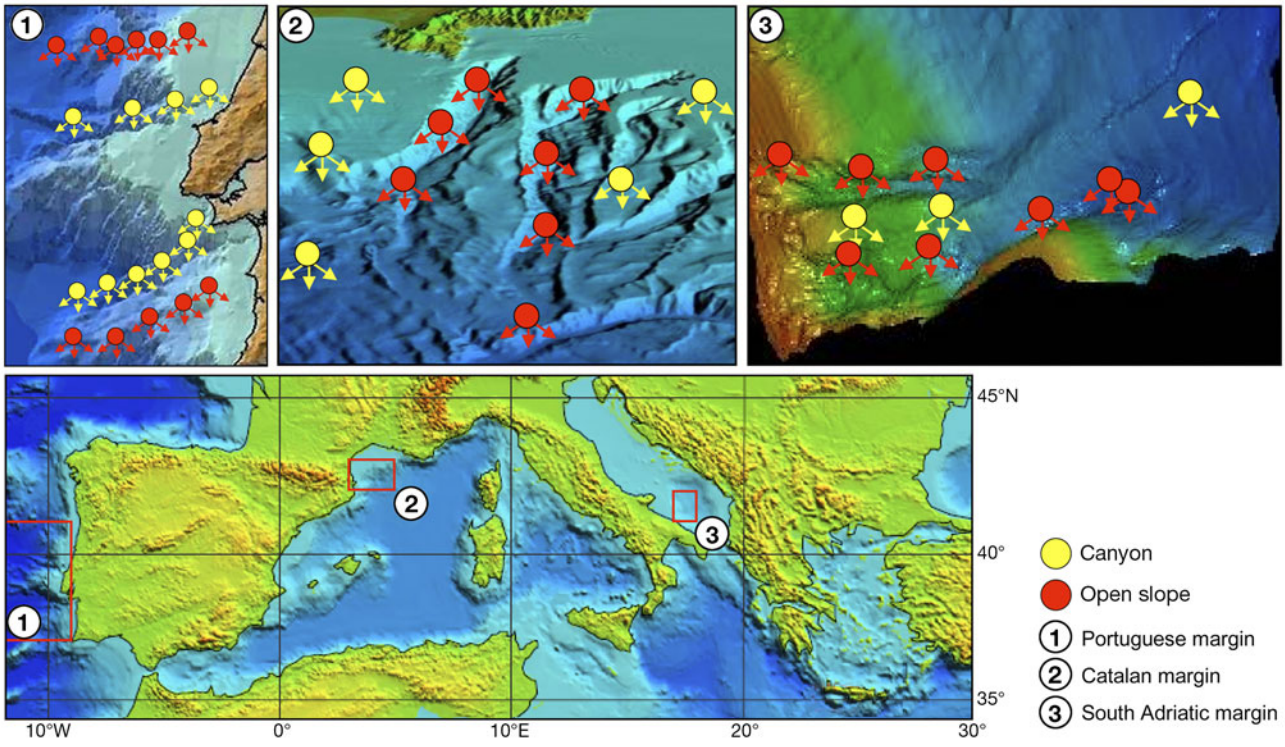

Fig. 1. Sampling areas and station locations. Arrows represent the 3 deployments performed at each station. Black in Panel 3: no bathymetric data

specimens per sample) were withdrawn and mounted on slides following the formalin-ethanol-glycerol technique described by Seinhorst (1959) to prevent dehydration. Nematodes were identified to species level (indicated as sp1, sp2, sp3, etc., due to the presence of several unknown deep-sea species) according to Platt & Warwick (1983, 1988), Warwick et al. (1998) and the recent literature dealing with new nematode genera and species (NeMys database, Deprez et al. 2005).

Nematode diversity was estimated using species richness (SR), defined as the total number of species identified at each station. Since species richness is strongly affected by the sample size, in order to standardise the values of nematode diversity, the expected number of species, ES(x), was considered. At each site, the species abundance data were converted into rarefaction diversity indices (Sanders 1968, as modified by Hurlbert 1971). The expected number of species for a theoretical sample of 100 specimens, ES(100), was selected to facilitate comparison of diversities from different regions. Species diversity (H', using log-base 2, H'^2) was measured by the Shannon-Wiener information function and species evenness was measured using J' (Pielou 1975). All indices reported above were calculated using PRIMER v5 (Clarke 1993). All diversity indices were calculated from the sum of the individuals of the 3 replicates of each sampling station.

We measured point, local (α), regional (γ) and biogeographical (ε) diversity; as inventory diversity measures they provide information on the species richness in an area at different spatial scales. All of these measures are expressed as nematode species abundance (Gray 2000). We also measured turnover diversity among sample diversity measures (β diversity) and turnover diversity among γ diversity measures (δ diversity) as diversity-differentiation measures, as they provide indications of the change in species composition among samples (β diversity) and regions (δ diversity). β and δ diversity were measured using similarity percentage (SIMPER) analyses and expressed as percentage of dissimilarity, based on a Bray-Curtis similarity matrix (Gray 2000).

The trophic composition of nematode assemblages was defined according to Wieser (1953). Nematodes were divided into 4 original groups as follows: (1A) no buccal cavity or a fine tubular one, selective (bacterial) feeders; (1B) large but unarmed buccal cavity, non-selective deposit feeders; (2A) buccal cavity with scraping tooth or teeth, epistrate or epigrowth (diatom) feeders; (2B) buccal cavity with large jaws, predators/omnivores. Moens & Vincx (1997) and Moens et al. (1999) proposed a modified feeding-type classification based on: (1) microvores; (2) ciliate feeders; (3) deposit feeders sensu stricto; (4) epigrowth feeders; (5) facultative predators and (6) predators. However, in the present study, Wieser's (1953) classification was preferred because it

is still widely used and no feeding-type information was available for most genera encountered in deep-sea systems in order to use the classification by Moens & Vincx (1997) and Moens et al. (1999).

The index of trophic diversity (ITD) was calculated as 1 – ITD, where ITD = $g_1^2 + g_2^2 + g_3^2 \ldots + g_n^2$, where g is the relative contribution of each trophic group to the total number of individuals and n is the number of trophic groups (Gambi et al. 2003). For n = 4 (as in the present study) 1 – ITD ranges from 0.00 to 0.75.

To identify colonization strategies of nematodes, the maturity index (MI) was calculated according to the weighted mean of the individual genus scores: MI = $\Sigma v(i)f(i)$, where v is the c – p value (colonisers – persisters) of genus i (as given in the Appendix of Bongers et al. 1991) and $f(i)$ is the frequency of that genus.

Statistical analyses. To test for bathymetric changes in the richness of higher meiofaunal taxa and nematode diversity indices in canyon and open slope sediments, a 1-way ANOVA was carried out for all of the measured indices separately for all of the canyons and open slopes, using stations (sampling depth) as random factors. When significant differences were encountered, a Student-Newman-Keuls (SNK) post hoc comparison test (at α = 0.05) was also carried out to ascertain in which transect values significantly changed with water depth.

PRIMER v5 software (Clarke 1993) was used to calculate Bray-Curtis similarities between all sampling sites. The obtained similarity matrix was used to produce a non-metric multidimensional scaling (NMDS) 2-dimensional plot. SIMPER analyses (based on the Bray-Curtis similarity index) were performed to estimate the β and δ diversity (i.e. turnover diversity estimated as % Bray-Curtis dissimilarity; Gray 2000) in meiofaunal taxonomic composition and nematode species composition between sampling depths within the same transect, between canyons and open slopes within the same region and among different regions (PRIMER v5; Clarke 1993). Analysis of similarities (ANOSIM) was performed to test for the presence of statistical differences in meiofaunal taxonomic composition and nematode species composition between sampling depths within the same transect, between canyons and open slopes within the same region and among different regions (PRIMER v5; Clarke 1993). All absolute data were presence/absence transformed prior to the analysis.

In order to assess how well the environmental constraints explained changes in biodiversity indices, non-parametric multivariate multiple regression analyses based on Bray-Curtis distances were carried out using the routine DISTLM forward (McArdle & Anderson 2001). The forward selection of the predictor variables was carried out with tests by permutation; p-values were obtained using 4999 permutations of raw data for the marginal tests (tests of individual variables), while for all of the conditional tests, the routine used 4999 permutations of residuals under a reduced model. We used water depth, bottom temperature, bottom salinity and sediment grain size as environmental parameters; phytopigment and biopolymeric C concentrations as indicators of the amount of trophic resources; and phytopigment to biopolymeric C ratio, protein to biopolymeric C ratio and carbohydrate to biopolymeric C ratio as indicators of the quality of trophic resources (for more details see Pusceddu et al. in press).

RESULTS

Bathymetric gradients of meiofaunal biodiversity along continental margins

Meiofaunal higher taxa richness and nematode diversity (expressed as SR, ES(100), H'^2, J', 1 – ITD and MI) are reported in Table 1. SR of nematodes ranged between 29 and 111 in the Portuguese margins, between 57 and 81 in the Catalan margins and between 15 and 82 in the South Adriatic margin. Significant changes in nematode diversity with increasing water depth were observed only in ~50% of the investigated systems, but the bathymetric patterns were not consistent between habitats (canyons versus slopes) or among regions (Table 2). In the S Portuguese and N Catalan slopes and the Cap de Creus/Sete and S Adriatic B canyons, the diversity indices decreased with increasing water depth, while they increased in the S Catalan slope and the Nazaré and S Adriatic C canyons. Finally, no significant bathymetric differences were observed in any of the other transects.

The SIMPER analysis, carried out for each transect, revealed that the dissimilarity among stations (β diversity) ranged from 32 to 57% for meiofaunal higher taxa, and from 51 to 80% for nematode species composition (Table 3). The ANOSIM analysis on each transect revealed the lack of significant differences in meiofaunal taxa composition among different depths ($p > 0.05$, ns; Table 3), but the presence of significant differences in terms of nematode species composition in almost all of the transects ($p < 0.01$; Table 3).

1 – ITD (0.28 to 0.74) and MI (2.13 to 3.21) did not display clear spatial patterns along the bathymetric gradients in each region (Table 1).

Richness of meiofaunal higher taxa and nematode biodiversity

Canyons and open slopes

At approximately equal depths, the richness of meiofaunal higher taxa and nematode species richness did

Table 1. Richness of meiofaunal higher taxa and nematode diversity indices in the study regions. SR: species richness; ES(100): expected species number for 100 individuals; H'^2: Shannon's index; J': species evenness; 1 – ITD: index of trophic diversity; MI: maturity index

Transect	Depth (m)	Richness of meiofaunal higher taxa	SR	ES(100)	H'^2	J'	1–ITD	MI
Portuguese margin								
Northern open slope	416	8	111	65.45	41.11	0.94	0.71	2.69
	959	13	95	58.10	36.64	0.92	0.66	2.69
	1463	8	75	63.31	35.11	0.95	0.71	2.81
	3475	9	102	63.30	39.22	0.94	0.72	2.71
	3981	7	94	55.63	35.43	0.91	0.69	2.66
	4902	7	93	54.80	34.55	0.90	0.72	2.75
Nazaré canyon	458	10	29	18.65	9.61	0.64	0.28	2.13
	897	7	50	33.46	22.70	0.84	0.74	2.87
	3231	8	50	33.90	21.75	0.83	0.69	2.69
	4363	5	49	35.30	23.15	0.86	0.71	2.80
Cascais	445	10	49	33.86	23.21	0.86	0.63	2.43
	1021	15	41	27.77	18.17	0.80	0.64	2.72
	2100	10	54	35.66	24.23	0.86	0.73	2.72
	2975	7	55	36.42	23.76	0.84	0.68	2.96
	3914	9	60	37.57	23.66	0.82	0.66	2.77
	4689	4	42	32.28	21.66	0.86	0.72	3.00
Southern open slope	1002	11	76	48.18	30.47	0.88	0.62	2.74
	2130	12	99	57.36	37.13	0.92	0.61	2.67
	2908	7	72	50.35	32.17	0.92	0.62	2.77
	3958	10	86	53.84	34.39	0.91	0.68	2.72
	4987	8	86	52.62	33.71	0.90	0.70	2.78
Catalan margin								
Northern open slope	334	14	80	49.18	33.30	0.91	0.71	2.78
	1022	6	66	43.00	29.36	0.90	0.73	2.90
Lacaze-Duthiers canyon	434	15	61	39.63	26.66	0.87	0.69	2.61
	990	14	62	39.14	25.98	0.86	0.69	2.60
	1497	9	64	43.25	27.77	0.88	0.71	2.78
Cap de Creus/ Sete canyon	960	8	81	47.56	31.45	0.88	0.71	3.04
	1434	7	59	36.86	24.13	0.84	0.66	2.69
	1874	5	57	43.14	27.38	0.90	0.71	2.82
	2342	10	70	44.02	29.91	0.89	0.70	2.97
Southern open slope	398	10	63	41.00	27.19	0.87	0.68	2.82
	985	11	68	42.33	27.64	0.86	0.69	2.73
	1887	10	80	48.53	32.73	0.90	0.70	2.93
South Adriatic margin								
Canyon B	370	5	65	48.69	29.81	0.91	0.71	3.02
	446	8	56	33.33	20.04	0.77	0.54	3.21
	590	7	56	40.85	26.82	0.89	0.65	2.77
Open slope	196	7	75	49.51	31.43	0.90	0.70	2.92
	406	7	57	39.19	25.50	0.87	0.72	2.63
	908	6	62	39.72	23.46	0.81	0.61	2.83
Canyon C	341	6	15	15.00	11.81	0.88	0.60	3.39
	435	7	47	39.16	25.16	0.90	0.67	2.69
	593	8	59	41.59	27.67	0.89	0.69	2.95
	618	7	54	34.55	21.62	0.81	0.59	2.90
	721	12	82	50.38	32.23	0.89	0.66	2.93

not display significant differences between canyons and adjacent open slopes within the same region (Table 1). The SIMPER and ANOSIM analyses, performed at 500, 1000 and 2000 m depths to assess the dissimilarity in meiofaunal higher taxa and nematode species composition between canyons and open slopes (β diversity), are reported in Table 4. At all sampling depths, the dissimilarity between canyons and open slopes was extremely high — on average 87% in the Portuguese margin, 51% in the Catalan margin and 60% in the South Adriatic margin — whilst the dissimilarity in terms of meiofaunal higher taxa was much lower (Table 4).

The ANOSIM analysis between canyons and open slopes revealed the lack of significant differences in the meiofaunal taxa composition within each investigated region at equal depths (i.e. 500, 1000 and 2000 m; ANOSIM, $p > 0.05$, ns; Table 4). Conversely, the ANOSIM analysis revealed significant differences between canyons and open slopes in the nematode species composition only in the Portuguese margin (ANOSIM, $p < 0.01$; Table 4).

Deep-sea regions

The richness of meiofaunal higher taxa and nematode species richness, on average, slightly decreased from the northeastern Atlantic to the central Mediterranean margin (Fig. 2). The analysis of meiofaunal assemblage composition confirmed the dominance of nematodes, copepods and polychaetes at all of the investigated deep-sea regions, but nematode species composition demonstrated the dominance of different species in different regions (Table 5 & Appendix 1).

At each water depth (i.e. 500, 1000 and 2000 m), significant differences among different regions were observed in terms of meiofaunal higher taxa and nematode species composition (ANOSIM, $p < 0.01$; Table 6). The dissimilarity of nematode species composition among different deep-sea regions (δ diversity), measured using the SIMPER analysis, was extremely high even when the analysis was restricted to equal water depths (i.e. 500, 1000 and 2000 m). The dissimilarity in species composition between the Portuguese margin and the Mediterranean regions was, on average, 90% and

Table 2. 1-way ANOVA carried out separately in all bathymetric transects testing for changes along a water depth gradient. SR: species richness; ES(100): expected species number for 100 individuals; H'^2: Shannon's index; J': species evenness; SNK: Student-Newman-Keuls test; ***p < 0.001; **p < 0.01; *p < 0.05; ns: not significant. +: increasing values with increasing water column depth; –: decreasing values with increasing water column depth

Transect	Richness of higher taxa			SR			ES(100)			H'^2			J'		
	F	p	SNK	*F*	p	SNK	*F*	p	SNK	*F*	p	SNK	*F*	p	SNK
Portuguese margin															
N Portuguese slope	0.62	ns	ns	0.39	ns	ns	0.39	ns	ns	0.75	ns	ns	1.68	ns	ns
Nazaré canyon	2.21	ns	ns	13.87	***	+	13.87	***	+	53.56	***	+	24.84	***	+
Cascais canyon	2.46	ns	ns	1.94	ns	ns	1.97	ns	ns	1.83	ns	ns	1.60	ns	ns
Catalan margin															
S Portuguese slope	6.85	***	–	2.93	ns	ns	2.93	ns	ns	1.72	ns	ns	0.57	ns	ns
N Catalan slope	57.80	***	–	7.90	*	–	5.22	ns	ns	2.63	ns	ns	0.23	ns	ns
Lacaze-Duthiers canyon	3.82	ns	ns	0.57	ns	ns	0.52	ns	ns	0.41	ns	ns	0.47	ns	ns
Cap de Creus/Sete canyon	2.91	ns	ns	10.38	***	–	10.40	**	–	10.38	**	–	6.19	*	–
S Catalan slope	0.60	ns	ns	5.73	*	+	6.22	*	+	2.91	ns	ns	1.37	ns	ns
South Atlantic margin															
Canyon B	1.82	ns	ns	6.93	*	–	6.93	*	–	6.73	*	–	6.28	*	–
S Adriatic slope	1.95	ns	ns	0.85	ns	ns	0.85	ns	ns	1.32	ns	ns	2.05	ns	ns
Canyon C	14.56	***	+	14.58	***	+	14.58	***	+	14.09	***	+	1.54	ns	+

Table 3. ANOSIM and SIMPER to test for differences in meiofaunal higher taxonomic composition and nematode species composition along a bathymetric gradient in each transect. Avg. diss.: average dissimilarity; ***p < 0.001; ns: not significant

Transect	Meiofauna			Nematode		
	ANOSIM		SIMPER	ANOSIM		SIMPER
	R	p	Avg. diss. (%)	R	p	Avg. diss. (%)
Portuguese margin						
N Portuguese slope	0.13	ns	40.18	0.09	ns	70.97
Nazaré	0.34	ns	27.38	0.39	***	79.83
Cascais	0.35	ns	34.71	0.28	ns	58.74
S Portuguese slope	0.16	ns	36.89	0.27	***	63.62
Catalan margin						
N Catalan slope	1.00	***	43.63	0.54	***	51.57
Lacaze-Duthiers	0.26	ns	42.73	0.28	ns	56.79
Cap de Creus/Sete	0.31	ns	36.74	0.61	***	55.43
S Catalan slope	0.74	***	43.70	0.92	***	51.31
Catalan margin						
B canyon	0.11	ns	56.54	0.63	***	55.74
S Adriatic slope	0.07	ns	34.83	0.87	***	70.43
C canyon	0.22	ns	32.30	0.62	***	67.10

between the western and central Mediterranean ~83%, whereas the dissimilarity of higher taxa composition was again lower (Table 6). The NMDS ordination plot based on these results pointed out that differences among deep-sea regions were more important than differences between habitats (e.g. canyon versus slope; Fig. 3).

The patterns of nematode species richness at larger spatial scales (i.e. habitat and regional scale) including all sampling depths are illustrated in Fig. 4a–c. The habitat diversity was similar in open slopes and canyons of the Mediterranean regions (Fig. 4a), but not in the Atlantic margin, where it was higher in the open slopes. Regional diversity (γ-diversity, Fig. 4b) was higher in the Portuguese margin than the other 2 investigated regions. Overall, nematode ε diversity (biogeographical diversity) was higher in the northeastern Atlantic than in the Mediterranean Sea (Fig. 4c). The results of the multivariate multiple regression analyses (DISTML) carried out using the biodiversity indices from the entire data set revealed that most of the variance could be explained by temperature, bottom salinity, grain size and a combination of pigment, proteins and biopolymeric C concentration ('All sites' in Table 7).

DISCUSSION

Bathymetric gradients in α diversity in deep-sea margins

Several studies have hypothesised that different factors, such as habitat heterogeneity (Levin et al. 2001, Vanhove et al. 2004) and changes in food availability and supply (Lambshead et al. 2000, 2002), can influence deep-sea biodiversity distribution. Since food in-

Table 4. ANOSIM and SIMPER to test for differences in meiofaunal higher taxonomic composition and nematode species composition at each selected water column depth (i.e. 500, 1000 and 2000 m) between canyons and open slopes within the same region. Avg. diss.: average dissimilarity; ***p < 0.001; ns: not significant; na: not available

Depth and transect	Meiofaunal ANOSIM R	p	SIMPER Avg. diss. (%)	Nematode ANOSIM R	p	SIMPER Avg. diss. (%)
500 m						
Portuguese	0.44	ns	28.72	0.83	***	83.28
Catalan	0.44	ns	28.07	0.83	ns	50.27
South Adriatic	0.44	ns	27.53	0.83	***	56.44
1000 m						
Portuguese	0.35	ns	41.24	0.69	***	84.97
Catalan	0.35	ns	41.02	0.69	ns	48.52
South Adriatic	0.35	ns	44.41	0.69	ns	59.01
2000 m						
Portuguese	0.64	ns	40.94	0.673	***	83.92
Catalan	0.64	ns	37.53	0.673	ns	54.19
South Adriatic	0.64	na	na	0.673	na	na

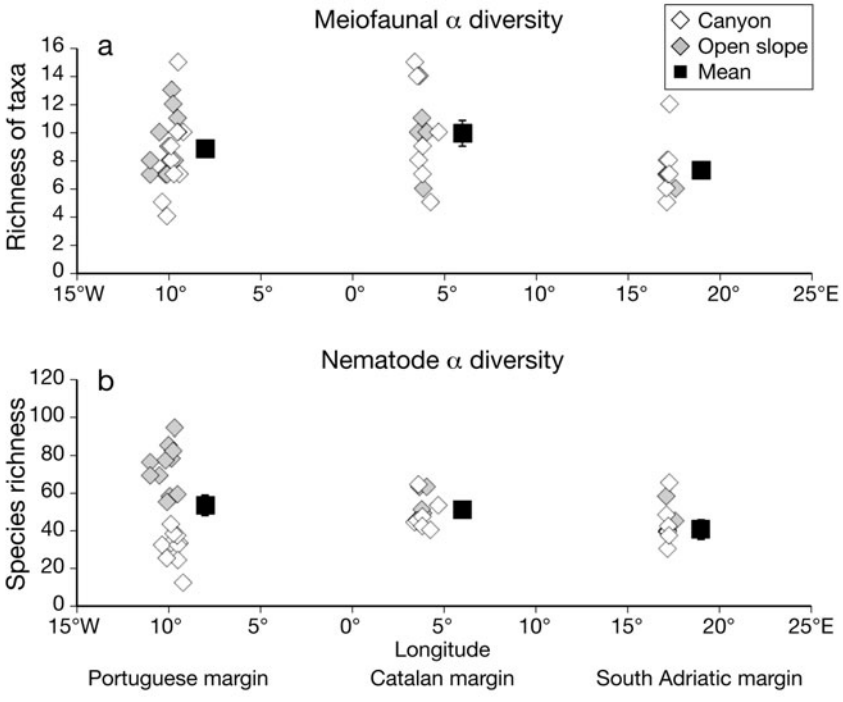

Fig. 2. α-diversity in different deep-sea regions measured as (a) richness of meiofaunal higher taxa and (b) nematode species richness. White diamonds indicate stations within canyons, grey diamonds indicate stations within open slopes and black squares indicate the mean ± SE

puts can change with increasing water depth, bathymetric gradients could reflect changes in the amount and quality of available food (Danovaro et al. 1999). A recent study reported that nematode biodiversity changed with water depth, and that bathymetric gradients were higher than changes observed at large spatial scales (>2500 km distance) at equal depths (Danovaro et al. 2008a). However, investigations conducted in a hadal trench of the South Pacific Ocean revealed that differences in water depth were responsible for significant differences in nematode species richness when food availability was not a limiting factor (Gambi et al. 2003).

Results presented here indicate that meiofaunal higher taxa richness and nematode species richness changed significantly with increasing water depth in about half of the investigated transects, but did not show consistent patterns. In fact, in both open slopes and canyons, increasing and decreasing patterns in species richness were observed (Table 2). These results are in agreement with the lack of consistent patterns in trophic resources (Pusceddu et al. in press), which showed the presence of increasing or decreasing concentrations of sediment organic matter in different transects independently from the regions (northeastern Atlantic, western and central Mediterranean) or habitats (slopes, canyons) investigated. The multivariate, multiple regression analyses indicated that quantity and quality of organic matter explained an important portion of the variances of the diversity indices, but temperature and physicochemical conditions also played an important role in determining the observed patterns. In addition, the analysis of nematode biodiversity revealed the presence of significant differences in species composition at different depths at all of the investigated transects, indicating that, independently from the presence of a significantly different species richness or organic matter content, bathymetric differences were always associated with significant changes in species composition (Table 3).

α, β and γ diversity in deep-sea margins

The comparison of the nematode diversity (as nematode species richness) at equal depths (i.e. separately at 500, 1000 and 2000 m depth, Fig. 2) revealed that the Portuguese margin contained the highest point diversity (number of species in a single sample) and that

Table 5. Meiofaunal higher taxa found in the 3 study regions

Taxon	%
Portuguese margin	
Nematoda	89.414
Copepoda	7.201
Polychaeta	2.124
Kinorhyncha	0.420
Oligochaeta	0.242
Ostracoda	0.186
Tardigrada	0.088
Bivalvia	0.070
Isopoda	0.063
Nemerta	0.058
Cumacea	0.038
Turbellaria	0.028
Amphiopoda	0.015
Tanaidacea	0.010
Acarina	0.008
Echinodermata larvae	0.008
Gastrotricha	0.005
Priapiluda	0.005
Priapulida larvae	0.005
Gnatostomulida	0.005
Sipunculida	0.003
Holothurians	0.003
Cnidaria	0.003
Catalan margin	
Nematoda	91.121
Copepoda	4.934
Polychaeta	1.600
Nemerta	1.136
Oligochaeta	0.271
Kinorhyncha	0.211
Ostracoda	0.129
Cumacea	0.120
Isopoda	0.108
Turbellaria	0.077
Bivalvia	0.069
Priapiluda	0.056
Tardigrada	0.052
Echinodermata	0.043
Gastrotricha	0.030
Amphiopoda	0.026
Tanaidacea	0.013
Sipunculida	0.004
South Adriatic margin	
Nematoda	93.751
Copepoda	3.066
Polychaeta	1.029
Priapiluda larvae	0.847
Tardigrada	0.504
Kinorhyncha	0.407
Decapoda larvae	0.150
Isopoda	0.086
Bivalvia	0.043
Ostracoda	0.032
Cnidaria	0.032
Oligochaeta	0.021
Cumacea	0.021
Acarina	0.011

such biodiversity showed a tendency to decrease moving eastward. However, despite such differences, the values of α diversity (richness of meiofaunal higher taxa or nematode species in 3 replicates from 1 site) were, on average, similar in all of the study regions.

The values of α diversity (nematode Shannon diversity) reported in the present study are higher than those reported by Garcia et al. (2007) for the Portuguese margin. Such a discrepancy could be due to different environmental factors, sampling seasons or sampling mesh sizes (20 versus 48 µm, respectively, which could have led to retain also the smallest organisms).

Overall, the richness of meiofaunal higher taxa and the biodiversity of nematodes did not show significant differences when canyons and adjacent open slopes were compared. Only along the Portuguese margin and at 500 m depth in the South Adriatic margin was nematode diversity significantly lower in canyons than in slopes (in agreement with Garcia et al. 2007, Ingels et al. 2009 who found lower diversity in the Nazaré canyon than in the adjacent open slope). Since higher concentrations of potential food resources were found in the Portuguese canyons than in the adjacent open slopes (for more details see Pusceddu et al. in press), the results of the present study provide further evidence that the amount of sediment organic matter is not sufficient to explain the observed changes in benthic biodiversity. The lower nematode biodiversity observed in canyons could be due to the presence of peculiar hydrodynamic conditions (Garcia et al. 2007), which could allow the colonization of a lower number of species. However, topographic features could also contribute to the differences as observed in the South Adriatic margin at 500 m depth; for instance, the lower nematode species richness in canyon C could be related to the presence of hard substrates (Trincardi et al. 2007). Overall, results presented here are in good agreement with previous studies, which reported that canyons were characterized by higher faunal abundance and biomass but lower diversity (Gage et al. 1995, Vetter & Dayton 1998, Curdia et al. 2004).

The analysis of functional (trophic) diversity and life strategies (1 – ITD and MI) did not display clear differences between canyons and slopes in any of the study regions. The maturity index always displayed intermediate values of 2.5 to 3.0, indicating that the nematode assemblages were characterized by a mixture of colonisers and persisters, both in canyons and open slopes of all regions (Gambi et al. 2003, Danovaro et al. 2008a).

Values of β diversity were always very high, but the dissimilarity in nematode species composition between canyons and open slopes of the Portuguese margin (~87%) was much higher than the dissimilarity measured in the margins of the Mediterranean Sea (range

Table 6. SIMPER and ANOSIM of the dissimilarity in meiofaunal higher taxonomic and nematode species composition between the study regions at equal sampling depths. Avg. diss.: average dissimilarity; ***p < 0.001; **p < 0.01; ns: not significant; na: not available

Depth	Region	Meiofauna			Nematode		
		ANOSIM		SIMPER	ANOSIM		SIMPER
		R	p	Avg. diss. (%)	R	p	Avg. diss. (%)
500 m	Portuguese vs Catalan	0.1	ns	37.8	0.7	***	93.0
	Portuguese vs S Adriatic	0.3	**	38.0	0.6	***	91.0
	Catalan vs S Adriatic	0.7	**	50.0	0.9	***	83.0
1000 m	Portuguese vs Catalan	0.0	ns	24.5	0.6	***	91.0
	Portuguese vs S Adriatic	0.5	***	50.1	0.4	***	89.0
	Catalan vs S Adriatic	0.5	***	42.0	0.9	***	82.0
2000 m	Portuguese vs Catalan	0.7	**	50.4	0.8	***	89.0
	Portuguese vs S Adriatic	na	na	na	na	na	na
	Catalan vs S Adriatic	na	na	na	na	na	na

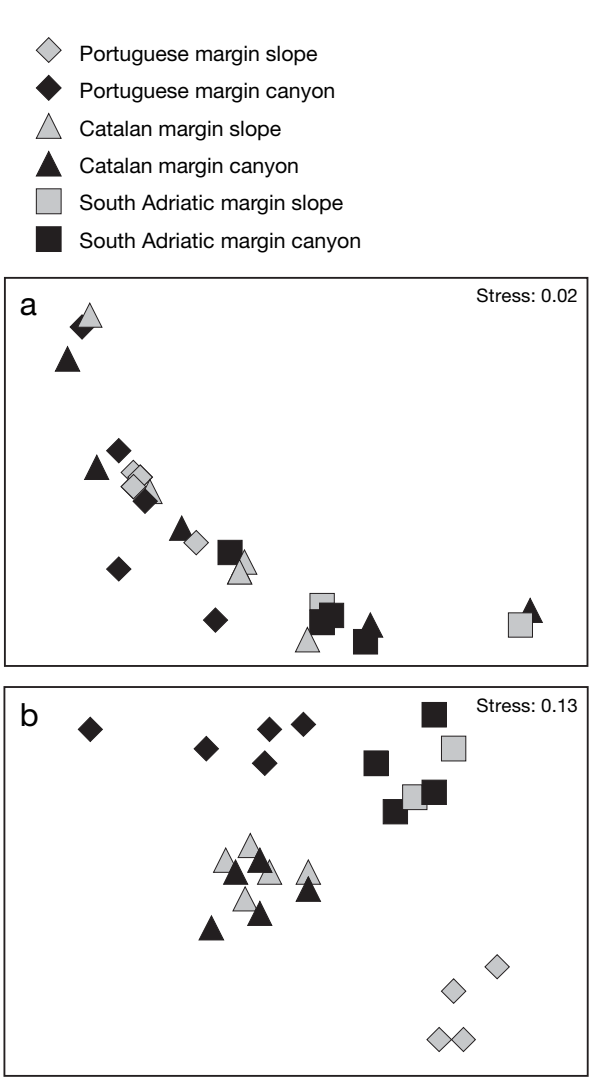

Fig. 3. Non-metric multidimensional scaling plot showing the similarity in (a) meiofaunal taxonomic composition and (b) nematode species composition between canyons and open slopes considering equal water column depths (i.e. 500, 1000 and 2000 m)

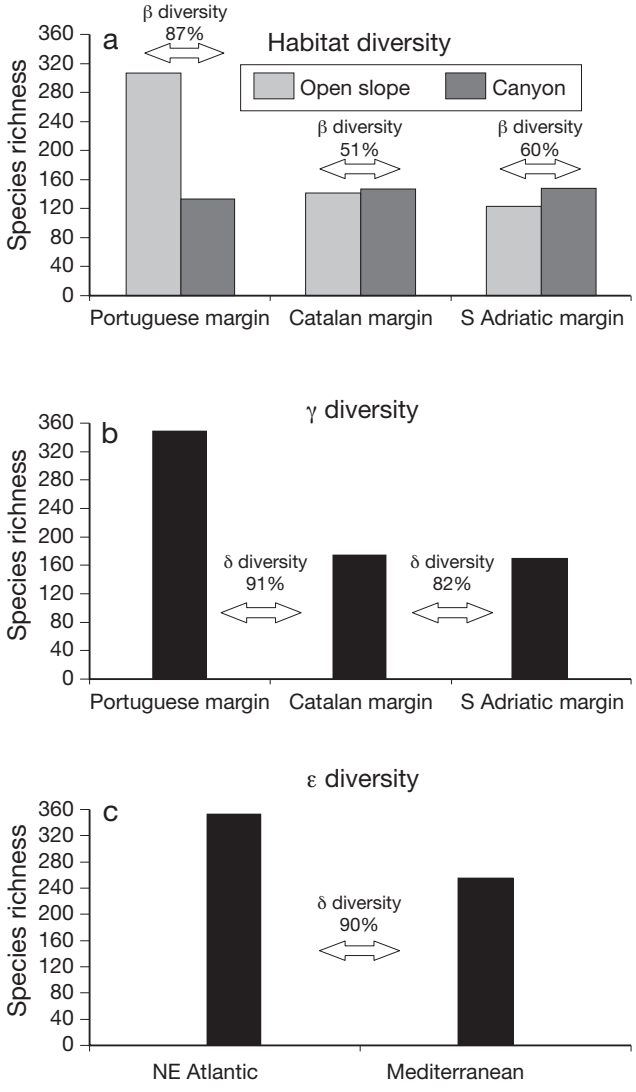

Fig. 4. Species richness of nematodes at different spatial scales: (a) habitat diversity; (b) γ diversity (regional) and (c) ε diversity (biogeographical). In (c), 'NE Atlantic' corresponds to the Portuguese margin and 'Mediterranean' includes the Catalan and South Adriatic margins

Table 7. Multivariate multiple regression analysis carried out on the values of the biodiversity indices at all sites, canyons and open slopes. % Var: percentage of explained variance. ***p < 0.001; **p < 0.01; *p < 0.05

Variable	SS	*F*	p	% Var	Cumulative %
All sites					
Pigment	4960.7	21.4	***	14.1	14.1
Silt %	3058.1	14.6	***	8.7	22.8
Bottom salinity	803.2	3.9	***	2.3	25.1
Bottom temperature	874.0	4.4	**	2.5	27.6
Biopolymeric C	1045.2	5.4	**	3.0	30.6
Protein to biopolymeric C ratio	243.4	1.3	**	0.7	31.3
Pigment to biopolymeric C ratio	123.8	0.6	ns	0.4	31.6
Water depth	71.3	0.4	ns	0.2	31.9
Protein to carbohydrate ratio	23.5	0.1	ns	0.1	31.9
Sand %	0.0	0.0	ns	0.0	31.9
Canyons					
Sand %	4308.9	16.7	***	18.6	18.6
Pigment	2626.7	11.6	***	11.3	29.9
Bottom salinity	567.8	2.6	ns	2.5	32.4
Protein to biopolymeric C ratio	392.0	1.8	ns	1.7	34.1
Biopolymeric C	299.7	1.4	ns	1.3	35.4
Pigment to biopolymeric C ratio	304.4	1.4	ns	1.3	36.7
Bottom temperature	95.5	0.4	ns	0.4	37.1
Water depth	22.8	0.1	ns	0.1	37.2
Silt %	0.0	0.0	ns	0.0	37.2
Protein to carbohydrate ratio	2.4	0.0	ns	0.0	37.2
Slopes					
Protein to carbohydrate ratio	695.2	7.3	**	11.7	11.7
Bottom salinity	158.5	1.7	ns	2.7	14.3
Pigment to biopolymeric C ratio	76.6	0.8	ns	1.3	15.6
Bottom temperature	283.1	3.1	ns	4.7	20.3
Pigment	64.2	0.7	ns	1.1	21.4
Protein to biopolymeric C ratio	55.8	0.6	ns	0.9	22.4
Silt %	46.5	0.5	ns	0.8	23.1
Biopolymeric C	10.3	0.1	ns	0.2	23.3
Water depth	7.7	0.1	ns	0.1	23.4
Sand %	0.0	0.0	ns	0.0	23.4

51 to 60%). Such differences in turnover diversity were responsible for the higher values of γ diversity (i.e. the regional diversity; Fig. 4b) of the Atlantic margin (349 species, ca. double that in the Catalan or the S Adriatic margins — 174 and 170 species, respectively).

δ and ε diversity in deep-sea margins

The δ-diversity, measured as turnover of nematode species among different regions (Portuguese versus Catalan versus S Adriatic) was always >80%, with highest differences between the 'cold' deep Atlantic and the 'warm' deep Mediterranean (>91%). Since the deep Atlantic and deep Mediterranean basins are physically separated by the Strait of Gibraltar and display enormous differences in terms of deep-water temperatures (~10°C), the differences in species composition between the 2 regions (δ diversity) are not surprising. But the high δ diversity between western and central Mediterranean systems (~82%) suggests that the difference in temperature is not the only driver of turnover diversity among regions. Rather, these results suggest that each deep-sea region is characterised by the presence of a specific assemblage and species composition. These results are confirmed by the NMDS analysis, which showed the presence of strong differences among the investigated regions in terms of richness of meiofaunal higher taxa and nematode species composition (Fig. 3), even when the analysis was performed at equal depths (i.e. 500, 1000 and 2000 m).

As a result of the important differences observed among the western and central Mediterranean regions, the overall differences in species richness (ε diversity) of the deep northeastern Atlantic and Mediterranean basins were less pronounced than those observed in terms of γ diversity. Overall, on the basis of the station samples (23 stations in the deep Mediterranean versus 21 in the deep Atlantic) the ε diversity of the deep Mediterranean basin was only 27% lower than that of the deep Atlantic. At the same time, it should be taken into account that the depth ranges of the 2 systems were different: 200 to 2000 m depth for the Mediterranean stations and 500 to 5000 m depth for the Atlantic. Since we demonstrated here that bathymetric differences are a key source of turnover diversity, it is possible that the quantitative differences reported are also influenced by the differences in extensions and depth ranges between the Atlantic and the Mediterranean margins. Overall, the data on nematode ε diversity in the deep sea suggest that, conversely to what was expected, the meiofauna and, particularly, nematode diversity of the deep Mediterranean basin is highly diversified and, thus, the deep Mediterranean is not biodiversity-depleted, but rather a diversity-rich biogeographical province.

The results of the present study indicate that differences in β and δ diversity and not α diversity are crucial to set-up or describe the deep-sea biodiversity at a regional scale, and that the analysis of the factors driving turnover diversity are crucial for a predictive understanding of the spatial patterns and species composition of deep-sea assemblages in different biogeographic regions.

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Appendix 1. Nematode species found in the 3 study regions. Only those species comprising >0.5% of the total are reported

Species	%	Species	%	Species	%
Portuguese margin		**Catalan margin**		**South Adriatic margin**	
Sabatieria sp1	4.76	*Sabatieria* sp1	6.88	*Pierrickia* sp3	10.87
Halalaimus sp4	4.00	*Theristus* sp1	4.95	*Aegialoalaimus* sp4	5.56
Halalaimus sp1	3.46	*Sabatieria* sp2	4.25	*Halalaimus* sp4	5.05
Acantholaimus sp4	3.03	*Halalaimus* sp7	3.75	*Sphaerolaimus* sp2	4.45
Acantholaimus sp1	2.94	*Prochromadorella* sp1	3.63	*Pierrickia* sp4	4.36
Actinonema sp1	2.83	*Halalaimus* sp4	3.54	*Pierrickia* sp2	3.59
Daptonema sp1	2.34	*Sabatieria* sp3	3.49	*Halalaimus* sp1	2.95
Metadesmolaimus sp2	2.29	*Pierrickia* sp1	3.34	*Sabatieria* sp1	2.95
Metalinhomoeus sp1	2.29	*Sphaerolaimus* sp1	3.28	*Desmoscolex* sp2	2.87
Pierrickia sp1	2.14	*Aegialoalaimus* sp1	2.84	*Amphimonhystrella* sp1	2.57
Linhystera sp1	2.10	*Daptonema* sp1	2.64	*Spilophorella* sp1	2.52
Pierrickia sp3	2.06	*Desmoscolex* sp1	2.52	*Syringolaimus* sp4	2.48
Aegialoalaimus sp1	1.92	*Aponema* sp1	2.11	*Desmoscolex* sp1	2.23
Amphimonhystrella sp1	1.86	*Actinonema* sp1	1.93	*Pierrickia* sp1	1.97
Pierrickia sp2	1.73	*Acantholaimus* sp1	1.87	*Actinonema* sp1	1.88
Sphaerolaimus sp3	1.62	*Amphimonhystrella* sp1	1.76	*Sabatieria* sp3	1.88
Longicyatholaimus sp1	1.52	*Sphaerolaimus* sp3	1.76	*Innocuonema* sp1	1.63
Theristus sp3	1.49	*Cyartonema* sp3	1.70	*Sphaerolaimus* sp1	1.63
Sphaerolaimus sp4	1.26	*Theristus* sp3	1.58	*Sabatieria* sp4	1.37
Praecanthonchus sp1	1.19	*Elzalia* sp1	1.55	*Adoncholaimus* sp2	1.24
Sphaerolaimus sp1	1.19	*Acantholaimus* sp2	1.52	*Setosabatieria* sp1	1.16
Theristus sp5	1.15	*Pselionema* sp1	1.32	*Anoplostoma* sp1	1.03
Syringolaimus sp4	1.15	*Chromadora* sp1	1.26	*Acantholaimus* sp6	0.94
Microlaimus sp1	1.08	*Diplopeltoides* sp1	1.26	*Hopperia* sp1	0.90
Minolaimus sp1	1.08	*Paracanthonchus* sp3	1.26	*Microlaimus* sp1	0.81
Theristus sp2	1.04	*Hopperia* sp1	1.23	*Linhystera* sp2	0.77
Acantholaimus sp12	1.00	*Syringolaimus* sp1	1.23	*Oxystomina* sp1	0.77
Daptonema sp2	1.00	*Longicyatholaimus* sp1	1.20	*Richtersia* sp1	0.77
Theristus sp1	1.00	*Tricoma* sp1	1.11	*Sphaerolaimus* sp3	0.77
Microlaimus sp2	0.95	*Halalaimus* sp1	1.08	*Halichoanolaimus* sp4	0.73
Daptonema sp3	0.89	*Paracanthonchus* sp2	0.88	*Acantholaimus* sp5	0.68
Desmoscolex sp5	0.86	*Dichromadora* sp1	0.76	*Desmoscolex* sp3	0.64
Microlaimus sp5	0.86	*Amphimonhystrella* sp3	0.73	*Desmodora* sp3	0.60
Amphimonhystrella sp2	0.76	*Elzalia* sp2	0.73	*Elzalia* sp2	0.60
Linhystera sp2	0.76	*Terschellingia* sp1	0.73	*Acantholaimus* sp4	0.56
Marylynnia sp1	0.76	*Metadesmolaimus* sp1	0.70	*Chromadorella* sp1	0.56
Paralongicyatholaimus sp1	0.74	*Leptolaimus* sp1	0.67	*Latronema* sp3	0.56
Setosabatieria sp1	0.74	*Setosabatieria* sp1	0.67	*Linhystera* sp1	0.56
Spilophorella sp1	0.73	*Oxystomina* sp1	0.64	*Diplopeltoides* sp3	0.51
Acantholaimus sp3	0.67	*Sphaerolaimus* sp2	0.64	*Metacyatholaimus* sp1	0.51
Diplopeltoides sp1	0.65	*Adoncholaimus* sp2	0.62	*Southerniella* sp1	0.51
Halalaimus sp5	0.65	*Innocuonema* sp1	0.62		
Bathyeurystomina sp1	0.61	*Platycoma* sp1	0.62		
Oxystomina sp1	0.61	*Sabatieria* sp5	0.62		
Campylaimus sp1	0.60	*Pierrickia* sp2	0.56		
Halalaimus sp6	0.58	*Acantholaimus* sp3	0.53		
Monhystera sp1	0.56	*Acantholaimus* sp6	0.50		
Comesoma sp1	0.54	*Aegialoalaimus* sp2	0.50		
Desmoscolex sp3	0.54	*Daptonema* sp2	0.50		
Pomponema sp1	0.54	*Theristus* sp4	0.50		

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