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Living at highest latitudes—the meiofauna of the Langseth Ridge (Arctic Ocean)—taxa composition, distribution, diversity and comparison with other marine regions

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Abstract

The expedition PS101 of RV POLARSTERN in 2016 offered the first opportunity for quantitative comparisons of metazoan meiobenthos of three different seamounts along the Langseth Ridge (High Arctic). Three hypotheses were to be tested: the meiobenthic communities of the studied elevations do not differ: (H_01) in their composition and taxa diversity, (H_02) with respect to different substrate types, and (H_03) from communities of other seamounts. The comparisons led to the acceptance of H_01, but to the rejection of H_02, as the three substrate types investigated (spicule-tube mat, underlying sediment, bare sediment) do not harbour a uniform meiofaunal community, but different assemblages, both in terms of taxa composition, abundance and diversity. The examination of H_03 could only be carried out qualitatively and could therefore only reveal tendencies. The comparison with the 11 Atlantic and Mediterranean seamounts and islands examined so far showed that seven of the 27 recorded major taxa occur on all elevations. This contrasts with ten taxa that were only found sporadically (on one to four elevations) and 12 taxa that were found on five to eleven seamounts/islands. An additional latitudinal and bathymetric comparison based on densities of dominating Nematoda and Copepoda from the Atlantic High Arctic to the High Antarctic (including the eastern Mediterranean and deep-sea regions) revealed that the polar regions are characterised by distinctly higher densities of individuals than lower latitudes, and that the summits/sublittoral of the studied seamounts and islands can by no means be regarded as "oases" in a hostile deep sea surrounding them.

Keywords Community analyses · Copepoda · Deep sea · Meiobenthos · Nematoda · Seamounts

Introduction

The question of whether seamounts play a significant role in the dispersal of marine metazoan meiobenthos has been the subject of a wealth of studies in recent decades (e.g. George 2013 and references therein, Zeppilli et al. 2013; Packmor et al. 2015; Pointner 2015, 2017, 2018; Packmor and Riedl 2016; Packmor and George 2018; George et al.

2018; Yamasaki et al. 2018, 2019; Richter 2019; Richter and George 2019; Kieneke and Todaro 2021; George 2022; Trokhymchuk and Kieneke 2024; Kieneke et al. 2025). The background to these studies is the fact that many representatives of the meiofauna have a very wide and often even cosmopolitan distribution, particularly at the species level, although this group of organisms is characterised by properties that hinder widespread expansion: a very small body size (rarely longer than 1 mm), a life cycle strictly bound to the substrate, no planktonic life stages and only small numbers of offspring. This phenomenon, known as the "meiofauna paradox" (Giere 2009; Cerca et al. 2018), is exacerbated when widespread shallow-water and often sand-dwelling (interstitial) taxa are affected, for which the vastness of the predominantly silty deep sea should actually represent an insurmountable barrier (cf. George and Schminke 2002; Gad and Schminke 2004; George 2004; Giere 2009; Plum and George 2009; Packmor et al. 2015; Packmor and Riedl 2016; Yamasaki et al. 2019;

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Trokhymchuk and Kieneke 2024). However, recent studies provide evidence that the meiofauna paradox might not exist in the originally assumed "drastic" form (cf. e.g. Ptatscheck and Traunspurger 2020). Not only did supposedly disjunctive distribution patterns turn out to be continuous in the course of comprehensive sampling (e.g. Packmor et al. 2015; Packmor and Riedl 2016), but also that the dispersal mechanisms of meiofauna are more complex and diverse than previously assumed, that supposedly disjunct species actually consist of several cryptic species, and that a lack of taxonomic expertise can often lead to erroneous results (Cerca et al. 2018).

George (2013) has provided a comprehensive review of meiofauna research on seamounts. It shows that the number of seamounts studied to date—which is very low in respect of meiofauna—is limited to the subtropical and temperate latitudes of the northern hemisphere. Most of the meiofauna studies were conducted in the Atlantic, with a few others in the Pacific and the eastern Mediterranean (see George 2013 and references therein). Despite this paucity of studies on meiofauna occurring on seamounts and the shelf of oceanic islands, the role of such geological structures in conjunction with meiofaunal long-distance-dispersal cannot be underestimated: they simply separate large distances into shorter segments and thereby much likely facilitate a "stepping stone dispersal" (Gad and Schminke 2004). Thus, participation in RV POLARSTERN's cruise PS101 "KARASIK" to the Langseth Ridge, a southerly directed seamount chain as part of the larger Gakkel Ridge in the High Arctic Ocean (September 9–October 23, 2016; Boetius and Purser 2017), offered a favourable opportunity to include seamounts from this climatologically and hydrologically extreme region of the world in the comparative meiobenthic studies (cf. George et al. 2017). Furthermore, large areas of the entire ridge structure are colonised by a peculiar megafauna community dominated by a few species of Porifera and an associated, epizoic fauna (Boetius and Purser 2017). Debris of this community (i.e. sponge spicules and calcareous tubes of polychaetes) had formed a dense and felty mat over the actual sediment layer (Morganti et al. 2022), and we had the unique opportunity to study the possibly adopted meiofauna community of this peculiar biogenic substratum.

Apart from the description of *Echinoderes pterus* Yamasaki et al. (2018) (Kinorhyncha) from the Karasik Seamount including records and distributions of further kinorhynch species (Yamasaki et al. 2018), this is the first comprehensive meiobenthic community analysis of a seamount from a region located just 3° below the North Pole. The present study focusses on the major metazoan meiobenthic taxa found at the Langseth Ridge and comprises geographical (i) intra- and (ii) interregional, as well as (iii) substrate-specific comparisons. Hence, the present study serves to test three hypotheses:

$H_0 1$: The meiofauna assemblages of the six sampled areas at the LR do not differ in composition or taxa diversity.

$H_0 2$: The different substrates studied do not harbour different meiobenthic communities, neither in terms of taxa composition nor diversity.

$H_0 3$: The meiofaunal assemblages at the LR do not differ from those of other seamounts.

Materials and methods

Study area

The roughly V-shaped Langseth Ridge (87°N/62°E–85°55 'N/57°45'E) runs in a north–south direction and intersects the Gakkel Ridge and its axial valley almost vertically at 61.5°E (Fig. 1) (Boetius et al. 2017; Diehl et al. 2017).

Its part south of the Gakkel Ridge consists of three summits: The Northern Mount (NM; 86°51.86 'N 61°34'E), which rises to a water depth of 630.6 m and whose northern slope descends steeply into the 4000 m deep axial valley of the Gakkel Ridge, the Central Mount (CM; 86°47. 83 'N/61°54.52'E, − 3300 m to − 721.5 m water depth) and the actual Karasik Seamount south of the other two summits (KS; 86°42.38 'N/61°08.07'E), which can itself be subdivided into two peaks (Fig. 1). KS and CM are connected via a deeper-lying saddle (CM_{sd}; − 1055 m water depth) (e.g. Boetius and Purser 2017; Morganti et al. 2022). The KS is the highest of the three crests and rises from about 2500 m to 584.8 m water depth at its shallow-most point (cf. Boetius et al. 2017; Diehl et al. 2017; Morganti et al. 2022; Stratmann et al. 2022). All three elevations consist predominantly of volcanic rock, mostly at the graded and cliff-like slopes, or have a surface that is densely colonised with megafaunal sponges, especially at the summit areas, or covered with a layer of felt-like interwoven sponge needles and polychaete tubes (siboglinids and serpulids), several centimetres thick. This peculiar organic substratum has been termed "spicule-tube mat" (Morganti et al. 2022) and will be referred to as STM throughout this publication. However, there are also occasional silty, sandy and gravelly areas of seafloor along the Langseth Ridge (Diehl et al. 2017; Stratmann et al. 2022). As a kind of reference area to the summit and saddle regions, we have also sampled the southwestern slope of the Karasik Seamount (KS_{sl}, see Fig. 1) at depths between 1829 and 2016 m. The summits, the saddle and the slope are referred to as "areas" throughout the text.

Sampling and sample treatment

A camera-guided multicorer (MUC) was used for sampling the meiobenthic communities of the Langseth Ridge, a proven deep-sea sampling gear according to Barnett et al.
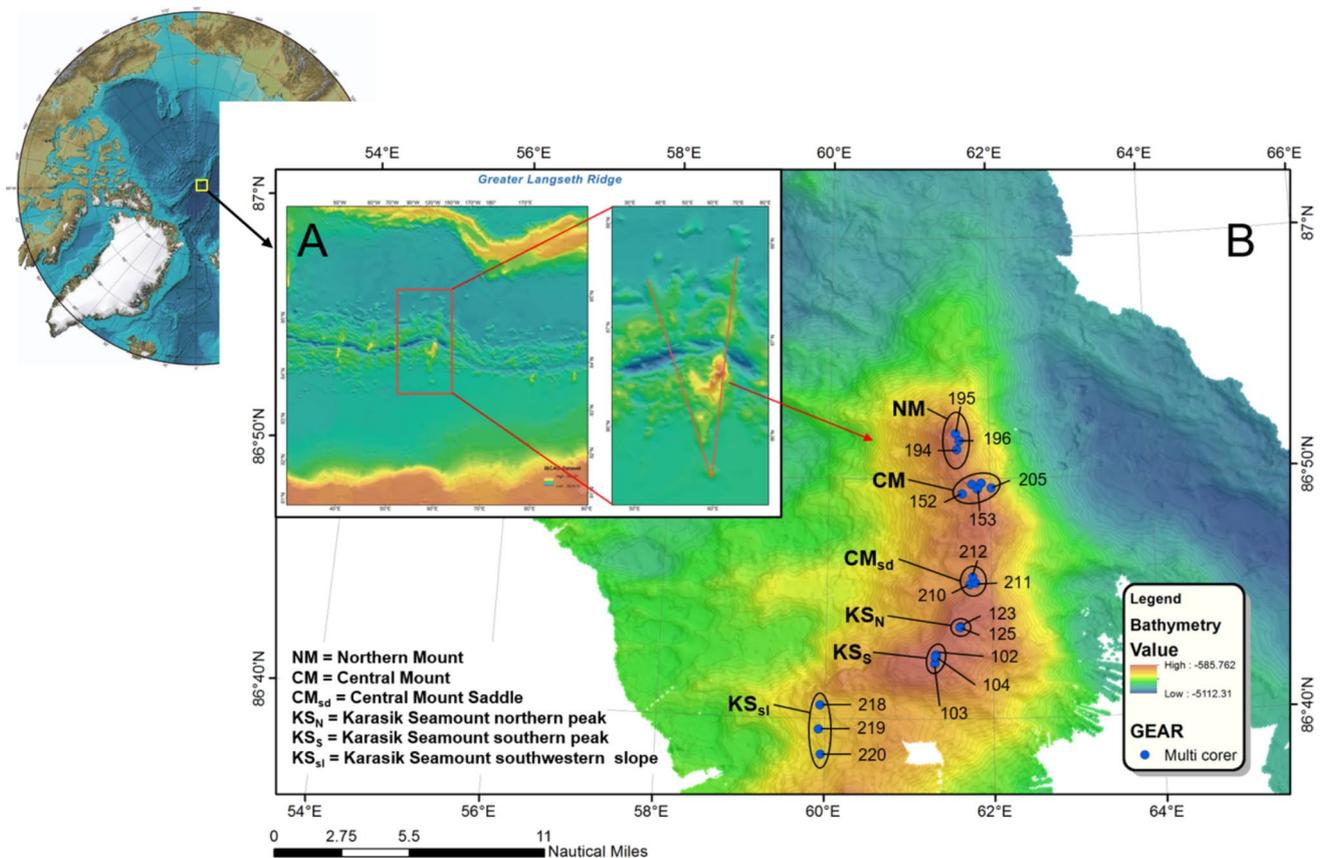
Fig. 1 HYPERLINK "sps:id::fig1|||locator::gr1|||MediaObject::0" Map of the southern Langseth Ridge, **A** Its position in the High Arctic Ocean, **B** The analysed meiofauna sampling stations (blue circles) at the three summits, a saddle area between two peaks and at the southern slope, collected with a multicorer during cruise PS101 of RV POLARSTERN in 2016. A. Modified from Boetius et al. (2017), B. Modified from George et al. (2017). Source of globe: http://gpsinformation.us/Maps/NorthPole

(1984) with an attached digital deep-sea camera capable to send live footage to the operation centre of RV POLARSTERN using the fibre optics wire (LWL). The MUC was additionally equipped with a POSIDONIA transponder for geo-referencing. Both live view from the seafloor and telemetry were mandatory for operating the deep-sea benthic sampling gear because of the ice drift that caused a permanent movement of the vessel of about 0.7 knots (Tardeck and Roessler 2017). The inner diameter of each core tubes is 9.4 cm; hence, each single tube sampled a surface of 69.36 cm^2 seafloor

After deployment of the MUC, each sediment core was immediately processed on board. For extraction of the whole meiofauna community at our home laboratory after the expedition, a slice of the upper 5 cm of each sediment core was cut without further sub-sectioning and filled into 750 ml Kautex® bottles. Several core samples were retrieved from areas where a layer of STM (varying thickness of up to 15 cm, see Morganti et al. 2022) was covering the actual sediment of the sea floor. In such cases, the whole STM was carefully separated from the sediment, and STM and underneath sediment were filled in separate Kautex® bottles. In the following, we refer to the STM as "Substratum A (Su$_A$)" and to the sediment layer underneath the STM as "Substratum B (Su$_B$)". Core samples that only contained soft sediment directly exposed to the water column (i.e. without a cover of STM) are referred to as "Substratum C (Su$_C$)" (Fig. 2). Such samples were obtained from the slope area, but also from the Northern Mount, the Central Mount and the Central Mount Saddle (Table 1). It has to be mentioned that some analysed core samples classified as Su$_C$ originate from MUC-deployments in areas with an incomplete, holey cover of STM, meaning adjacent core tubes of the same deployment contained a cover of STM. In particular, these samples (indicated wit C* in Table 1) are 153-1 (MUC 2 & 8), 196-1 (MUC 1 & 6) and 210-1 (MUC 2 & 5).

Fixation was carried out with borax-buffered formaldehyde solution at a final concentration between 4 and 8% (*v/v*). If a haul yielded enough undisturbed core samples, some were preserved with DESS, a solution of dimethyl sulfoxide, disodium EDTA and saturated NaCl. DESS was invented for simultaneous preservation of genomic DNA and
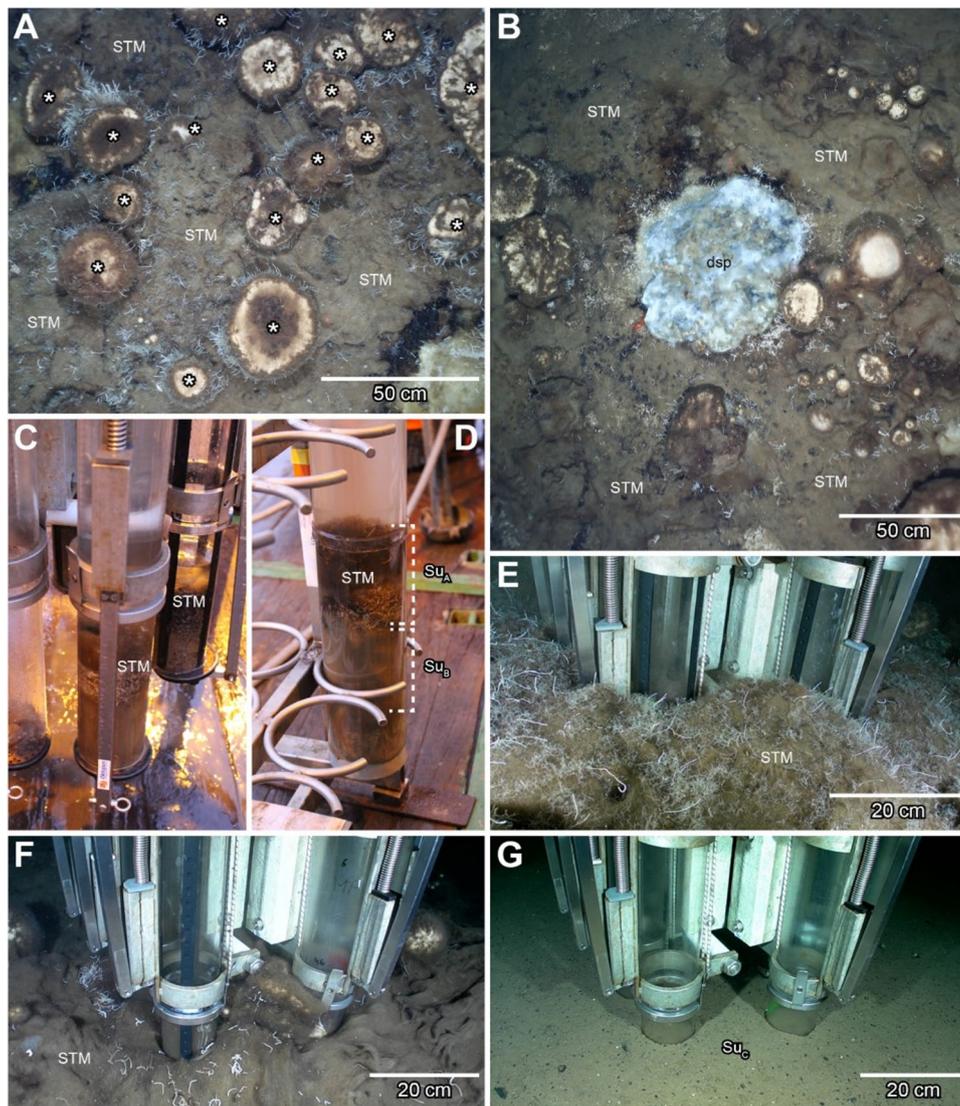
Fig. 2 Seafloor conditions of the central Arctic Langseth Ridge. **A** Still frame of video footage made with the Ocean Floor Observation System (OFOS) at the northern summit of Karasik Seamount (KS) during expedition PS101. The seafloor is densely colonised with megafaunal sponges (asterisks); between them spreads a felty spicule-tube-mat (STM), **B** OFOS image of the southern summit of KS with a huge decaying sponge (dsp) surrounded by STM and further intact sponges, **C, D** Core samples of the camera-guided multicorer (MUC) containing a layer of STM (=substratum A, Su_A) of varying thickness above the soft sediment (=substratum B, Su_B), **E** MUC-deployment at the southern summit of KS, **F** MUC-deployment at the saddle region between the Central Mount and KS, **G** MUC-deployment at the southwestern slope of KS that only consists of bare sediment (=substratum C, Su_C). A, B: deployments 120 and 100 of the OFOS, both images at about 900 m depth; C–G: deployments 101/104/104/212/220 of the MUC at 635/634/634/936/2016 m depth, respectively. Images A, B with courtesy of A. Purser (AWI, Bremerhaven); images C–G by F. Schramm (MPI for Marine Microbiology, Bremen)

for a good conservation of the morphology of nematodes (Yoder et al. 2006).

However, as a saturated saline, DESS significantly affects fragile and soft-bodied meiofauna organisms, and hence, the current study is mostly based on formaldehyde-fixed samples; only in the case of station #103, we needed to analyse one core tube fixed with DESS in order to have two tubes from that deployment. Before fixing each MUC core, either with formaldehyde or with DESS, the supernatant seawater was poured over a 40 µm sieve in order to catch epi-/hyperbenthic animals that might be present in the fine fluffy layer on top of the sediment. Subsequently, the catches of the sieve were rinsed into the sample bottle (in cases with a STM-cover to the bottle containing the Su_A). For most cores, the sieve and shovel were rinsed with a 7% (*w/v*) aqueous solution of $MgCl_2$ in order to anaesthetise the meiobenthic organisms prior to fixation. The sample was allowed to stand for approximately 10 min before the fixative was added to

Table 1 Station data of analysed deployments and core tubes of the multicorer of expedition PS101

Station	Area	Core	Substrate	Quantitative?	Fixation	Latitude (N)	Longitude (E)	Depth [m]
PS101/102–1	KS_S	MUC1	A & B	yes	$MgCL_2$ and FA	86° 42.68' N	061° 19.35' E	645
		MUC3	A & B	yes	$MgCL_2$ and FA			
PS101/103–1	KS_S	MUC1	A & B	yes	DESS	86° 42.56' N	061° 18.78' E	633
		MUC7	A & B	yes	$MgCL_2$ and FA			
PS101/104–1	KS_S	MUC6	A & B	yes	seawater and FA	86° 42.59' N	061° 18.62' E	634
		MUC8	A & B	yes	seawater and FA			
PS101/123–1	KS_N	MUC3	A & B	yes	seawater and FA	86° 43.83' N	061° 36.95' E	651
		MUC5	A & B	yes	seawater and FA			
PS101/125–1	KS_N	MUC6	A	yes	seawater and FA	86° 43.77' N	061° 36.76' E	664
		MUC6	B	yes	seawater and FA			
PS101/152–1	CM	MUC2	C	**no**	$MgCL_2$ and FA	86° 49.38' N	061° 40.16' E	892
		MUC4	C	yes	$MgCL_2$ and FA			
PS101/153–1	CM	MUC2	C*	**no**	$MgCL_2$ and FA	86° 49.56' N	061° 51.16' E	868
		MUC8	C*	**no**	$MgCL_2$ and FA			
PS101/194–1	NM	MUC3	A*	**no**	$MgCL_2$ and FA	86° 51.22' N	061° 34.87' E	732
		MUC5	A	**no**	$MgCL_2$ and FA			
PS101/195–1	NM	MUC3	C	yes	$MgCL_2$ and FA	86° 51.88' N	061° 34.61' E	638
		MUC8	C	yes	$MgCL_2$ and FA			
PS101/196–1	NM	MUC1	C*	yes	$MgCL_2$ and FA	86° 51.59' N	061° 37.09' E	655
		MUC6	C*	yes	$MgCL_2$ and FA			
PS101/205–1	CM	MUC5	C	yes	$MgCL_2$ and FA	86° 49.53' N	061° 59.54' E	1132
		MUC8	C	yes	seawater and FA			
PS101/210–1	CM_{sd}	MUC2	C*	yes	seawater and FA	86° 45.50' N	061° 43.39' E	1014
		MUC5	C*	yes	seawater and FA			
PS101/211–1	CM_{sd}	MUC2	A & B	yes	seawater and FA	86° 45.59' N	061° 47.85' E	927
		MUC6	A & B	yes	seawater and FA			
PS101/212–1	CM_{sd}	MUC2	A & B	yes	seawater and FA	86° 45.87' N	061° 45.54' E	936
		MUC6	A & B	yes	seawater and FA			
PS101/218–1	KS_{sl}	MUC2	C	yes	seawater and FA	86° 40.62' N	059° 56.70' E	1829
		MUC6	C	yes	seawater and FA			
PS101/219–1	KS_{sl}	MUC1	C	yes	seawater and FA	86° 39.64' N	059° 55.33' E	2005
		MUC5	C	yes	seawater and FA			
PS101/220–1	KS_{sl}	MUC2	C	yes	seawater and FA	86° 38.60' N	059° 56.86' E	2016
		MUC6	C	yes	seawater and FA			

NM Northern Mount, *CM* Central Mount, *CM_{sd}* Central Mount saddle, *KS_N* Karasik Seamount, northern peak, *KS_S* Karasik Seamount, southern peak, *KS_{sl}* Karasik Seamount slope

A, Su_A (STM); A*, Su_A of considerable thickness and sediment underneath not sampled; B, Su_B (sediment underneath STM, 0–5 cm); C, Su_C (bare sediment, 0–5 cm); C*, Su_C from areas with incomplete, holey STM-cover; DESS, dimethyl sulfoxide plus disodium EDTA plus saturated NaCl; FA, borax-buffered formaldehyde; N, north/northern; Quant., quantitative sampling; S, south/southern, STM, spicule-tube mat

Bold highlight's the names of the objects (in columns) and attributes (in rows)

the sample bottle. This step is recommended for soft-bodied meiofauna such as gastrotrichs in order to avoid body contractions or distortions due to muscle spasms (e.g. Todaro and Hummon 2008).

Fixed meiofauna specimens were separated from the sediment and the organic debris (i.e. STM) using the silica gel gradient centrifugation technique (Pfannkuche and Thiel 1988) with a suspension of the colloidal silica Levasil© plus an addition of Kaolinite (about two spoons per centrifuge beaker) and spinning the samples (each core sample was usually separated to four centrifuge bottles and later united again) using a Heraeus Megafuge 40 centrifuge (Thermo Scientific) at 3.608 rpm. The supernatant was poured again over a 32 μm sieve and rinsed to 100 ml Kautex® bottles, and a few drops of a Rose Bengal solution were added in order to stain the meiofauna organisms for a better recognition during sorting. In the case of the STM samples, the supernatant of the centrifugate was fractionally sieved over

32, 100 and 300 µm meshes in order to get rid of single sponge spicules that were resuspended during pouring out. For sorting and identification of meiofauna higher level taxa, subsamples were placed into a labyrinth chamber according to Bogorov (1927) and screened under dissecting microscopes with transmitted light illumination (Leica M80 or M125 stereo microscopes). Identification of taxa was aided by relevant literature (e.g. Higgins and Thiel 1988; Schmidt-Rhaesa 2020). For the current study, we have analysed the meiofauna composition of 17 MUC-deployments and 46 core (sub-) samples, with 15 of Su_A, 13 of Su_B and 18 of Su_C (Tab. 1, supplement S1).

Quantitative data analysis

Only three replicates were obtained in almost every area, and only two at the northern peak of KS (= KS_N). This low number allows neither a test for normal distribution nor a meaningful calculation of the arithmetic mean. However, the determination of the median Z did not provide any useful results either, as the range of variation between the replicates of an area was too large. It was therefore decided to calculate the specimen density D (ind./10 cm^2) for further analyses.

Faunistic comparison comprising diversity and similarity analyses as well as statistical tests (one-way ANOSIM) (Clarke 1993) was undertaken with the use of the statistical software package PAST 4.03 (Hammer et al. 1999–2022). Similarity analyses were made using the Bray–Curtis index (Bray and Curtis 1957) and the Cosine Similarity (e.g. Pfeifer et al. 1998; George 1999; Shimanaga et al. 2004; George et al. 2014). The reason for the chosen similarity measures will be substantiated below in the results section. For the estimation of taxa diversity, Shannon's H' and Pielou's Evenness J were calculated (Shannon and Weaver 1963; Pielou 1966). In order to visualise the diversity characteristics of the stations and to consider the fact that we could only analyse two instead of three replicates of KS_N, rarefaction analyses were performed (e.g. Hurlbert 1971; Achtziger et al. 1992; George 2005; George et al. 2014).

Results

A total of 22 major taxa were recorded in the study area (Fig. 3). They were distributed over 94,556 individuals from the 46 multicorer (sub-) samples. Of these, 282 could not be assigned to any animal group, so they were not included in the analyses. In addition, those animal groups that could not be determined beyond doubt (Ciliophora(?), Crinoida(?), Plathyhelminthes(?)) ($N_\Sigma = 105$) were also not considered.

Of the 19 taxa analysed ($N = 94,169$), Nematoda (Fig. 3F–H) made up by far the largest group with $N = 71,223$ (rel. ab. 75.63%), followed by Copepoda (Fig. 3A, B;

$N = 14,168$, 15.05%), Annelida ($N = 3,897$, 4.14%) and Tardigrada ($N = 2,756$, 2.93%) (Table 2, Fig. 2). With $N = 92,044$, these four taxa together account for 97.74% of all meiobenthic taxa. Of the remaining 15 taxa, Gastrotricha ($N = 771$) and Acari (Fig. C, D; $N = 737$) account for a further 1.6% with $N_\Sigma = 1,508$. In contrast, the remaining 13 major taxa combined ($N_\Sigma = 480$) account for only 0.66% of the meiofauna specimens found (Table 2, Fig. 4). These 13 taxa were summarised as "others (sum)" in the analysis.

Distribution of major taxa among the areas

To test H_0I, the findings in the NM, CM, CM_{sd}, KS_N, KS_S and KS_{sl} sites were compared with each other. Not all 19 major taxa were found in every area. Ten of the 19 taxa occur in all areas (but not in all stations), the others are distributed somewhat heterogeneously among areas and even stations and are absent in at least one site. Bivalvia and Rotifera could only be detected by singletons in one site (Table 2).

For further similarity analyses, the absolute abundance values were standardised to the density D (ind./10 cm^2) (Table 3). Nematoda show the highest values in all areas, followed by Copepoda (Fig. 5A). They also have the highest relative abundance, with the highest value (rel. ab. 90.83%) at KS_{sl} (Fig. 5B).

At the KS_S, on the other hand, they only achieved a relative abundance of 52.70%; here the Copepoda occur considerably more frequently and reach their highest value in the entire study area with a relative abundance of 27.65%. The Tardigrada (rel. ab. 12.11%) are the third most common taxon at the KS_S and also reach their highest value there (Fig. 5B).

With the clear differences in the composition and abundance of the taxa in the different areas, Fig. 5A already indicates that if a large-scale uniform meiofauna community exists at the LR, it might be characterised by heterogeneous assemblages, though.

Tables 2 and 3 show, however, that there are also differences in the composition of the taxa: Priapulida were found exclusively at the NM, whereas Cumacea, Bivalvia and Rotifera were found only at the Karasik Seamount (KS_N and KS_S). However, because representatives of these taxa were only found extremely rarely and in very small numbers, it remains open whether their absence at other stations could possibly be due to the small number of samples, so that they were simply not recorded there.

There is also no recognisable geographical gradient; however, Fig. 5A indicates that the communities of KS_N and CM_{sd} may be less productive than those to the south (KSS, KS_{sl}) and north (NM, CM). To investigate this in more detail, we performed a similarity analysis of the stations.

Fig. 3 Representatives of major taxa of the benthic meiofauna inhabiting the seafloor of the central Arctic Langseth Ridge. **A, B** Copepoda. **C, D** Acari. **E** Tanaidacea. **F–H** Nematoda. The displayed animals were extracted on board of RV POLARSTERN from a felty mat consisting of sponge spicules and calcareous tubes of polychaetes during expedition PS101 (deployments 101 and 125 of the multicorer at 635 and 664 m depth). Imaged aboard RV POLARSTERN with an Olympus CX 41 microscope
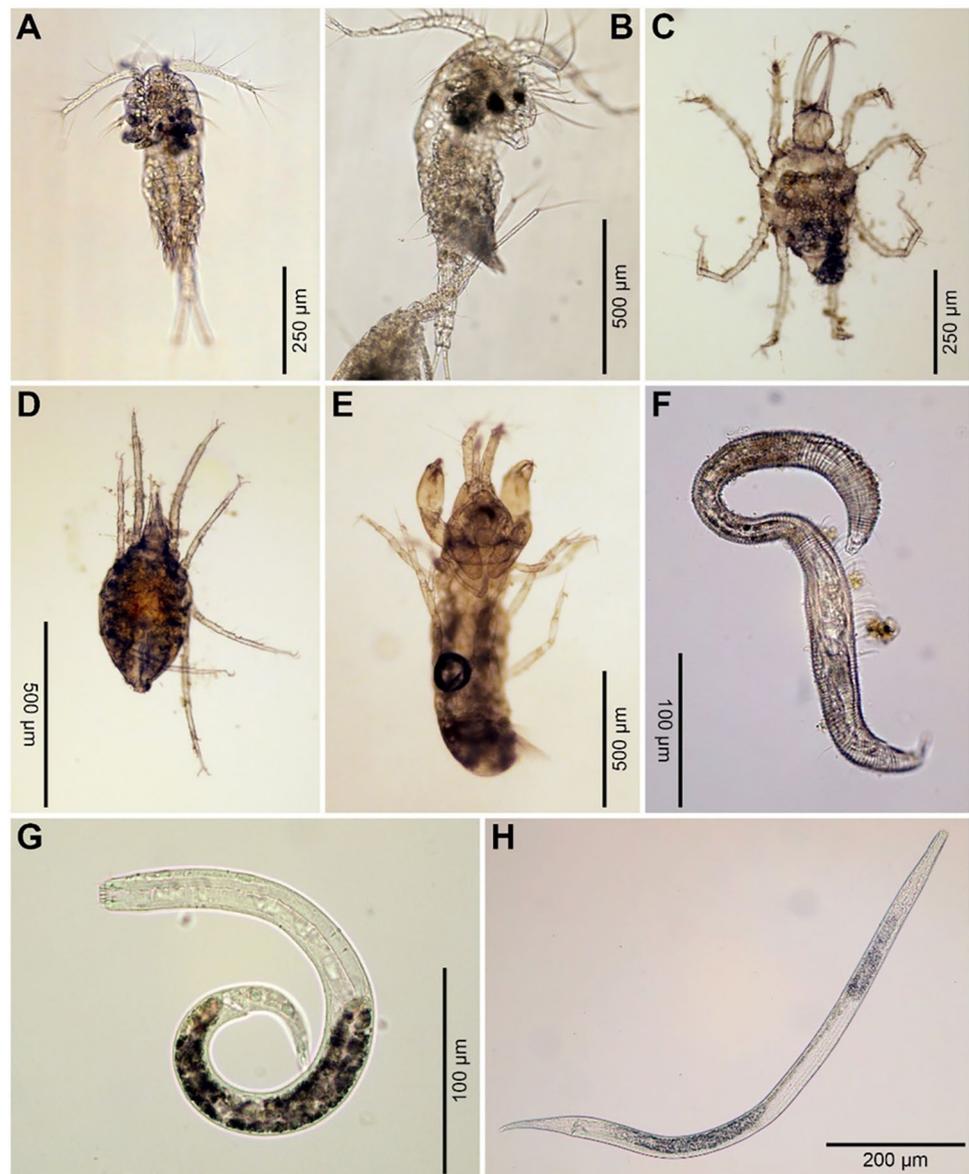
Distribution of major taxa among the stations

Similarity analyses

In the similarity analysis, we considered all stations and all 19 major taxa, even though Cumacea were represented by only two individuals, and Bivalvia and Rotifera by only one each. The remaining 16 taxa occurred everywhere or were distributed over several stations (Table 2). First, the Bray–Curtis index, based on the absolute abundance values, was calculated and subsequently visualised using non-metrical Multidimensional Scaling (nMDS). The nMDS plot shows a more or less uniformly mixed arrangement of the stations; there is no clear sorting along a geographical gradient or grouping of stations from one area (Fig. 6A).

Nevertheless, a certain trend can be recognised: Stations 102, 103, 194, 211 and 212 are located in the lower left-hand section of the plot, while the remaining stations are clearly separated from them. However, both groups are very heterogeneous, and similarities of stations between areas are always higher than within areas. An Analysis of Similarity (ANOSIM) confirmed this impression. The mean rank of the stations between the different areas ($r_b = 69.4$) and that of stations within an area ($r_w = 61.75$) are very close to each other and prove that the differences between stations in the same area and those in different areas are very similar. This is confirmed with $R = 0.1125$, whereby $p = 0.1869$ proves that even the separation of the two groups is not significant.

The Cosine Similarity was used in a second analysis to investigate the qualitative similarity of the taxon

Table 2 List of the meiobenthic taxa collected with the multicorer during research cruise PS101 of RV POLARSTERN in 2016 at different areas along the Langseth Ridge (central Arctic Ocean)

No	Taxa/Area	NM	CM	CM_{sd}	KS_N	KS_S	KS_{sl}	Sum	Rel. ab. (%)
1	Nematoda	14,021	16,394	7621	8589	8894	15,704	**71,223**	**75.63**
2	Copepoda	2702	2263	2832	1156	4667	548	**14,168**	**15.05**
3	Annelida	643	398	916	318	620	1002	**3897**	**4.14**
4	Tardigrada	82	140	410	78	2044	2	**2756**	**2.93**
5	Gastrotricha	221	24	100	62	356	8	**771**	**0.82**
6	Acari	177	105	25	267	162	1	**737**	**0.78**
7	*Cnidaria*	*19*	*12*	*11*	*1*	*91*	*3*	***137***	***0.15***
8	*Ostracoda*	*18*	*7*	*30*	*5*	*54*	*0*	***114***	***0.12***
9	*Kinorhyncha*	*0*	*92*	*4*	*0*	*1*	*0*	***97***	***0.10***
10	*Isopoda*	*23*	*1*	*3*	*6*	*32*	*14*	***79***	***0.08***
11	*Tanaidacea*	*13*	*5*	*3*	*22*	*18*	*4*	***65***	***0.07***
12	*Amphipoda*	*3*	*0*	*22*	*5*	*20*	*0*	***50***	***0.05***
13	*Tantulocarida*	*6*	*23*	*0*	*3*	*1*	*2*	***35***	***0.04***
14	*Loricifera*	*0*	*13*	*0*	*1*	*3*	*3*	***20***	***0.02***
15	*Gastropoda*	*0*	*6*	*0*	*0*	*2*	*2*	***10***	***0.01***
16	*Priapulida*	*6*	*0*	*0*	*0*	*0*	*0*	***6***	***0.01***
17	*Cumacea*	*0*	*0*	*0*	*0*	*2*	*0*	***2***	***0.00***
18	*Bivalvia*	*0*	*0*	*0*	*0*	*1*	*0*	***1***	***0.00***
19	*Rotifera*	*0*	*0*	*0*	*1*	*0*	*0*	***1***	***0.00***
Sum		*17,934*	*19,483*	*11,977*	*10,514*	*16,968*	*17,293*	*94,169*	*100.00*
No. taxa		*19*	*19*	*19*	*19*	*19*	*19*		
Others (sum 7–19)		*88*	*159*	*73*	*44*	*225*	*28*	*617*	*0.66*

Given are the absolute counts per studied area and altogether (sum), and the relative abundance (%)

NM Northern Mount, *CM* Central Mount, *CM_sd* Central Mount saddle, *KS_N* Karasik Seamount, northern peak, *KS_S* Karasik Seamount, southern peak, *KS_sl* Karasik Seamount slope

Less abundant taxa ($N < 700$) italics -marked and summed as "others (sum 7–19)"

Bold highlight's the names of the objects (in columns) and attributes (in rows)

composition, emphasising the distribution patterns of the most dominant taxa (Shimanaga et al. 2004). This approach resulted in a clear separation of the two groups of stations that had only been weakly divided by the Bray–Curtis index. At the bottom right of the ordination plot (Fig. 6B), 11 stations from all areas are closely packed together. It is also noticeable that stations of the same area are placed particularly close together (Fig. 6B, KS_{sl}, CM_{sd}). The close grouping of the right-hand group indicates an almost uniform community structure of the meiobenthos at the higher taxonomic level. On the other hand, four further stations (Fig. 6B: stations 102, 103, 211, 212) form a second grouping that is clearly distinct from the first, but the stations of this grouping are not as closely associated to each other as in the former.

However, it is recognisable that stations 211 and 212 (CM_{sd}) also lie very close together. And finally, station 194 and particularly station 104 appear very isolated, which was not the case when analysed with the Bray–Curtis index (cf. Fig. 6A). The subsequent ANOSIM confirmed the findings:

The $r_w = 49.31$ in comparison with the remarkably higher $r_b = 71.06$ points towards a generally greater similarity between stations of the same area than between stations from different areas. In our opinion, this can be explained by the close mutual proximity of the stations of KS_{sl}, CM and KS_N in the right-hand group, and of stations 211 and 212 as well as (to a lesser extent) of stations 102 and 103 in the left-hand group. The value of $R = 0.3198$ in turn indicates that despite the groupings described above, there is a fundamentally mixed distribution of the stations, which is also clearly recognisable in Fig. 6B, and with $p = 0.0145$ (threshold value: $p = 0.05$), this result is certified as significant.

Diversity analyses

A comparative diversity analysis of the areas using *S*, *H'* and *J* revealed the greatest diversity at the KS_S (Table 4, Fig. 7). In contrast, the other areas show variations between the different measures. With $S = 14$, KS_N and CM show the second highest number of detected major
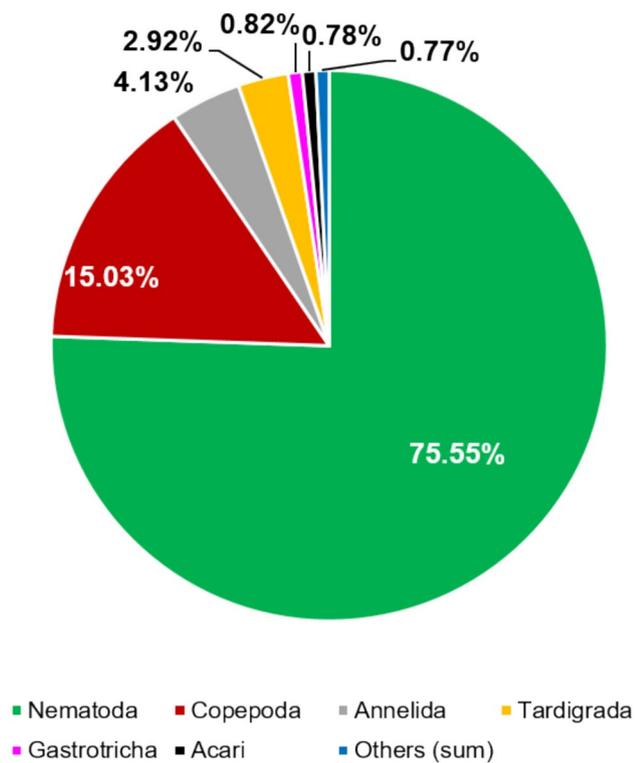
Fig. 4 Relative abundance values of meiofauna major taxa collected along the Langseth Ridge (central Arctic Ocean) on RV POLARSTERN cruise PS101 (2016). The group "Others (sum)" (0.51%) is composed of Amphipoda, Bivalvia, Cumacea, Gastropoda, Isopoda, Kinorhyncha, Loricifera, Ostracoda, Priapulida, Rotifera, Tanaidacea, Tantulocarida

taxa, but both are surpassed by NM as far as H' and J are concerned. The comparatively low H' value at KS_N can be explained by the fact that the number of individuals is lowest there (Table 4), which in turn is related to the fact that only two instead of three replicates could be analysed at the site. In addition, the individuals are very unevenly distributed among the species, which is expressed by the likewise low J-value.

The lowest diversity values were recorded at KS_{sl}, although a comparatively large number of individuals were found in this area (Table 4). This may be due to the fact that the otherwise very abundant Acari, Gastrotricha and Tardigrada were only detected in very low abundances at this site. Thus, despite the presence of 12 taxa, the KS_{sl} community is dominated with 99.77% by Nematoda, Copepoda and Annelida (see Table 2), explaining the low H' and J values.

The opposite appears to be the case for the CM_{sd}. With $S = 12$, it has just as few taxa as the KS_{sl}, and the number of individuals is the second lowest of all with $N = 11,977$ (Table 4). The H' and J values, on the other hand, are the second highest of all the sites. One explanation may be the comparatively abundant occurrence of taxa that are

otherwise among the rarest, particularly the Amphipoda and Ostracoda (Table 2).

Fluctuations regarding H' and J are particularly pronounced at the MN, the CM_{sd} and the KS_N (Fig. 7). In particular, the Evenness values J are remarkable. They basically follow the S and H' values and also show a fluctuation in the distribution of individuals among the taxa at the stations. Moreover, they are generally low (Table 5, Fig. 7) and thus confirm the observed high dominance of a few taxa (cf. Tables 2, 3).

The rarefaction analyses only partially confirm the results of the diversity coefficients. Although this method also approves that the KS_S has the highest diversity (Fig. 8A), it is nevertheless recognisable that the calculated H' and J values should be treated with caution, especially for the KS_N.

With respect to the CM_{sd}, it can be seen from the corresponding curve in Fig. 8A that an increase in individuals apparently does not lead to an associated increase in the number of taxa. The situation is different at KS_N: Despite the fact that only two instead of three replicates are present from this area (resulting in the lowest N of all areas), it can be seen by means of Rarefaction analysis that with a higher yield the KS_N might possibly have the next highest diversity (Fig. 8A), which could lead to the conclusion that the Karasik Seamount would be characterised by the highest taxa diversity along the Langseth Ridge.

However, there is consistency between the calculated diversity values and the Rarefaction analysis when comparing the stations. As Fig. 8B shows, the station curves of the same area are broadly fanned out, apart from those from KS_{sl}. This confirms the results presented in Table 5 and Fig. 7. They generally show that the meiobenthos along the Langseth Ridge is also highly heterogeneous in terms of diversity.

This could indicate that although a largely uniform meiofaunal community occurs at this ridge, it is heterogeneously distributed across the areas. Most of the stations are very similar in terms of composition and abundance, and the taxa diversity also shows only slight fluctuations. The heterogeneity of the individual assemblages is confirmed by the results of the similarity and diversity analyses (especially Rarefaction analysis). Both show that stations from different areas are often more similar to each other than to those in their own area; however, distinguishable communities could not be detected for the individual areas. Nevertheless, it should be noted that the observed fluctuations are not least due to the small number of samples. Sampling at more than three (KS_N: two) stations per area could certainly have provided clearer results. Furthermore, a comparison at the level of major taxa can only provide an initial indication of the faunistic conditions. Only at the species level will it be possible to determine whether the picture obtained here can also be confirmed with such a better taxonomic resolution.

Table 3 List of the meiobenthic major taxa collected with a multicorer at different areas along the Langseth Ridge (central Arctic Ocean) during PS101 (2016)

No	Taxa/station	NM 194	195	196	Mean	CM 152	153	205	Mean	CMsd 210	211	212	Mean
1	Nematoda	219.87	1346.45	455.16	673.83	937.57	493.94	932.09	787.87	550.46	199.39	348.90	366.25
2	Copepoda	219.29	69.35	100.92	129.85	165.80	55.07	105.39	108.76	80.88	121.83	205.59	136.10
3	Annelida	73.10	9.08	10.52	30.90	18.60	9.37	29.41	19.13	13.55	41.81	76.70	44.02
4	Tardigrada	3.75	1.73	6.34	3.94	8.22	8.07	3.89	6.73	10.24	17.01	31.86	19.70
5	Gastrotricha	20.04	0.58	11.25	10.62		3.03	0.43	1.73	3.17	8.79	2.45	4.81
6	Acari	1.30	3.89	20.33	8.51	8.94	5.19	1.01	5.05	1.44	0.43	1.73	1.20
7	*Cnidaria*	*2.45*		*0.29*	*1.37*	*0.14*	*0.87*	*0.72*	*0.58*	*0.43*	*0.43*	*0.72*	*0.53*
8	*Ostracoda*	*2.31*		*0.29*	*1.30*		*0.58*	*0.43*	*0.50*	*0.14*	*1.59*	*2.60*	*1.44*
9	*Kinorhyncha*					*11.25*	*1.59*	*0.43*	*4.42*	*0.58*			*0.58*
10	*Isopoda*	*1.15*	*0.43*	*1.73*	*1.11*		*0.14*		*0.14*			*0.43*	*0.43*
11	*Tanaidacea*	*1.15*	*0.29*	*0.43*	*0.62*	*0.29*	*0.43*		*0.36*		*0.43*		*0.43*
12	*Amphipoda*			*0.43*	*0.43*					*0.14*	*0.14*	*2.88*	*1.06*
13	*Tantulocarida*	*0.87*			*0.87*	*1.87*	*0.87*	*0.58*	*1.11*				
14	*Loricifera*					*1.01*	*0.14*	*0.72*	*0.62*				
15	*Gastropoda*					*0.43*		*0.43*	*0.43*				
16	*Priapulida*	*0.58*	*0.14*	*0.14*	*0.29*								
17	*Cumacea*												
18	*Bivalvia*												
19	*Rotifera*												
	Sum	**545.85**	**1431.95**	**607.84**	**861.88**	**1154.12**	**579.30**	**1075.55**	**936.32**	**661.04**	**391.87**	**673.88**	**575.60**
	No. Taxa	**12**	**9**	**12**	**13**	**11**	**13**	**12**	**14**	**10**	**10**	**10**	**11**
	Others (sum 7-19)	*8.51*	*0.87*	*3.32*	*4.23*	*14.99*	*4.61*	*3.32*	*7.64*	*1.30*	*2.60*	*6.63*	*3.51*

No	Taxa/station	KS_N 123	125	Mean	KS_S 102	103	104	Mean	KSsl 218	219	220	Mean
1	Nematoda	537.63	700.69	619.16	282.87	594.58	404.84	427.43	716.26	1004.18	543.69	754.71
2	Copepoda	98.33	68.34	83.33	171.86	397.78	103.23	224.29	31.00	22.64	25.37	26.34
3	Annelida	34.75	11.10	22.92	27.54	41.81	20.04	29.80	44.26	58.97	41.23	48.15
4	Tardigrada	4.76	6.49	5.62	61.56	61.56	171.57	98.23	0.29			0.29
5	Gastrotricha	8.79	0.14	4.47	13.70	24.37	13.26	17.11	0.58	0.29	0.29	0.38
6	Acari	17.16	21.34	19.25	13.70	4.04	5.62	7.79		0.14		0.14
7	*Cnidaria*	*0.14*		*0.14*	*2.74*	*6.78*	*3.60*	*4.37*				
8	*Ostracoda*	*0.14*	*0.58*	*0.36*	*2.74*	*3.03*	*2.02*	*2.60*				
9	*Kinorhyncha*				*0.14*			*0.14*				
10	*Isopoda*		*0.87*	*0.87*	*1.44*	*1.30*	*1.87*	*1.54*		*0.87*	*1.15*	*1.01*
11	*Tanaidacea*	*2.31*	*0.87*	*1.59*	*0.72*	*1.59*	*0.29*	*0.87*		*0.58*		*0.58*
12	*Amphipoda*	*0.29*	*0.43*	*0.36*	*0.58*	*0.87*	*1.44*	*0.96*				
13	*Tantulocarida*	*0.14*	*0.29*	*0.22*	*0.14*			*0.14*	*0.14*	*0.14*		*0.14*
14	*Loricifera*		*0.14*	*0.14*		*0.29*	*0.14*	*0.22*		*0.14*	*0.29*	*0.22*
15	*Gastropoda*				*0.29*			*0.29*	*0.29*			*0.29*
16	*Priapulida*											
17	*Cumacea*				*0.14*	*0.14*		*0.14*				
18	*Bivalvia*				*0.14*			*0.14*				
19	*Rotifera*	*0.14*		*0.14*								
	Sum	**704.58**	**811.27**	**757.93**	**580.31**	**1138.12**	**727.94**	**815.46**	**792.82**	**1087.95**	**612.46**	**831.07**
	No. Taxa	**12**	**12**	**14**	**16**	**13**	**12**	**17**	**7**	**9**	**6**	**11**
	Others (sum 7-19)	*3.17*	*3.17*	*3.82*	*9.08*	*13.99*	*9.37*	*11.41*	*0.43*	*1.73*	*1.44*	*2.23*

Given is the density D (ind./10 cm^2) in the single stations (all samples/subsamples per station combined) and the density mean in the corresponding areas

NM Northern Mount, *CM* Central Mount, *CM$_{sd}$* Central Mount saddle, *KS$_N$, KS$_S$* northern and southern peak of Karasik Seamount, *KS$_{sl}$* southern slope at Karasik Seamount

Fig. 5 Data of the meiofauna collected with the multicorer during cruise PS101 (2016), all stations and cores per area summed, **A** Density values (ind./10 cm^2), **B** Relative abundance values (%). For the most abundant taxa, the values are also given numerically. *NM* Northern Mount, *CM* Central Mount, *CM$_{sd}$* Central Mount saddle, *KS$_N$*, *KS$_S$* northern and southern peak of Karasik Seamount, *KS$_{sl}$* southern slope at Karasik Seamount
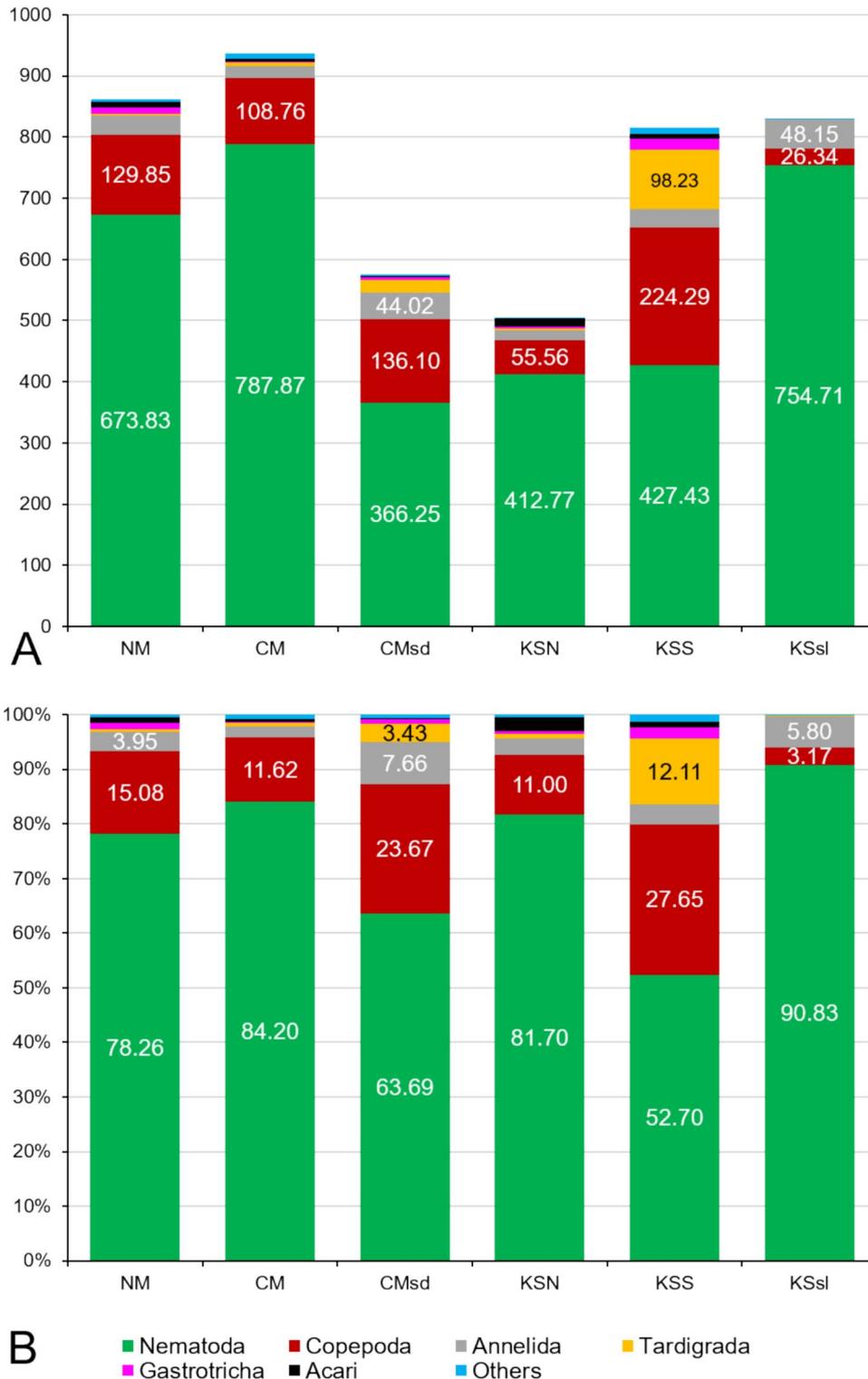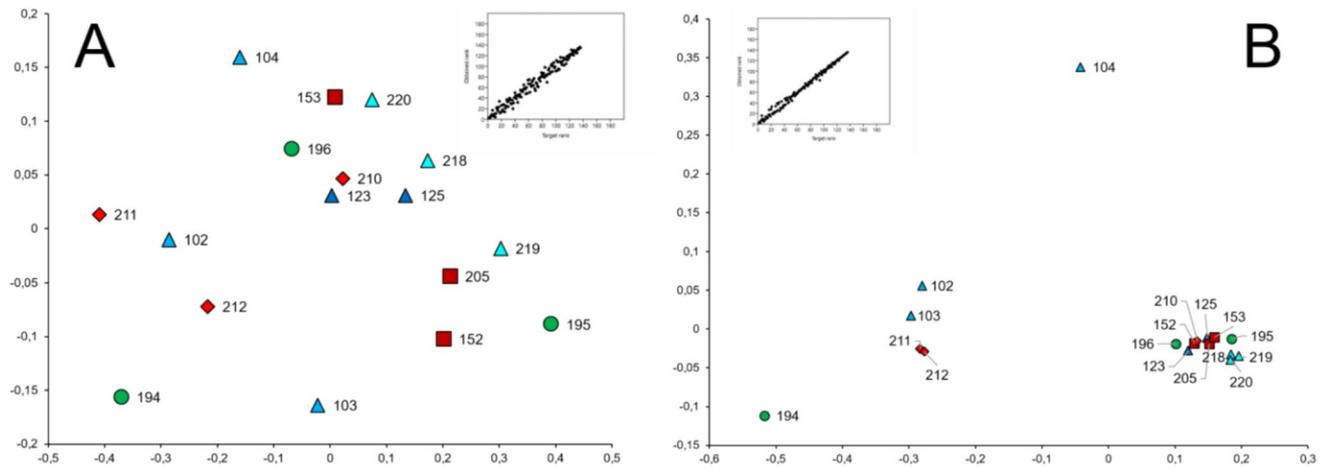
Fig. 6 Ordination plots of a non-metrical Multidimensional Scaling, showing the mutual (dis)similarity of the stations sampled along the Langseth Ridge, according to the composition and density (ind./10 cm.^{2}) of the meiobenthic major taxa found during cruise PS101 of RV POLARSTERN (2016). **A** Bray–Curtis index, stress = 0.08372. Top right: Shepard diagram, **B** Cosine Similarity index, stress = 0.04694. Top left: Shepard diagram. Triangles indicate the stations of Karasik Seamount (dark blue: KSN, blue: KSS, light blue: KSsl); red rhombs: CMsd; red squares: CM; green circles: NM)

Table 4 Results of a comparative diversity analysis of the areas sampled during cruise P101 of RV POLARSTERN (2016) along the High-Arctic Langseth Ridge

	NM	CM	CM$_{sd}$	KS$_N$	KS$_S$	KS$_{sl}$
S	13	14	12	14	17	12
N	17,934	19,483	11,977	10,514	16,968	17,293
H'	0.7561	0.5973	1.033	0.7031	1.274	0.3799
J	0.2948	0.2263	0.4159	0.2664	0.4496	0.1529

Given are the number of reported taxa S, the number of collected specimens N and the calculated diversity values of Shannon's H' and Pielou's Evenness J

NM Northern Mount, *CM* Central Mount, *CM$_{sd}$* Central Mount saddle, *KS$_N$*, *KS$_S$* northern and southern peak of Karasik Seamount, *KS$_{sl}$* southern slope at Karasik Seamount

However, on the basis of the available data, hypothesis $H_0 1$ is accepted: The meiobenthic assemblages of the six studied areas form a large community, which nevertheless is distributed very disparately across the Langseth Ridge.

Distribution of major taxa among different substrates

In addition to a possible geographical influence on the distribution and composition of the meiofauna at the LR ($H_0 1$), we investigated whether the composition of the substrate at the stations plays a role ($H_0 2$). During sampling, differences in the composition of the substrate were identified, which we characterised as follows (see also section "Materials and methods"):

- Substratum A (Su$_A$): A layer of STM with varying thickness that lay on top of the actual sediment;
- Substratum B (Su$_B$): The actual muddy sediment underneath the STM/Su$_A$ layer;

- Substratum C (Su$_C$): Exposed muddy seabed not covered by STM/Su$_A$.

The different substrate types were fixated and sorted separately; those samples that contained both Su$_A$ and Su$_B$ were divided to separate sample bottles (see also section "Materials and methods"). For the following analyses, the sampled stations were grouped according to their shares of the substrates. As a consequence, the number of analysed samples was greater than in the geographical analysis.

A first comparison of the distribution of the major taxa among the substrates revealed a pattern as graphically shown in Fig. 9A: 18 of the 19 taxa were found in Su$_A$, 11 in Su$_B$ and 16 in Su$_C$. Ten major taxa occurred in all substrates; six others were only found in Su$_A$ and Su$_C$. With Bivalvia and Rotifera, two taxa were restricted to Su$_A$, while the Cumacea could only be detected in Su$_B$. No taxon was found exclusively in Su$_C$. Thus, even at the level of major taxa, the following qualitative results were obtained: Apart from the taxa that were found in every substratum, no exclusive

Fig. 7 Results of a comparative diversity analysis for meiobenthos sampled during cruise P101 of RV POLARSTERN (2016) along the High-Arctic Langseth Ridge, showing the taxa numbers S, Shannon's H' and Pielou's J (means and standard deviations of the core samples per area) calculated for the areas. NM = Northern Mount, CM = Central Mount, CM_{sd} = Central Mount saddle, KS_N, KS_S = northern and southern peak of Karasik Seamount, KS_{sl} = southern slope at Karasik Seamount
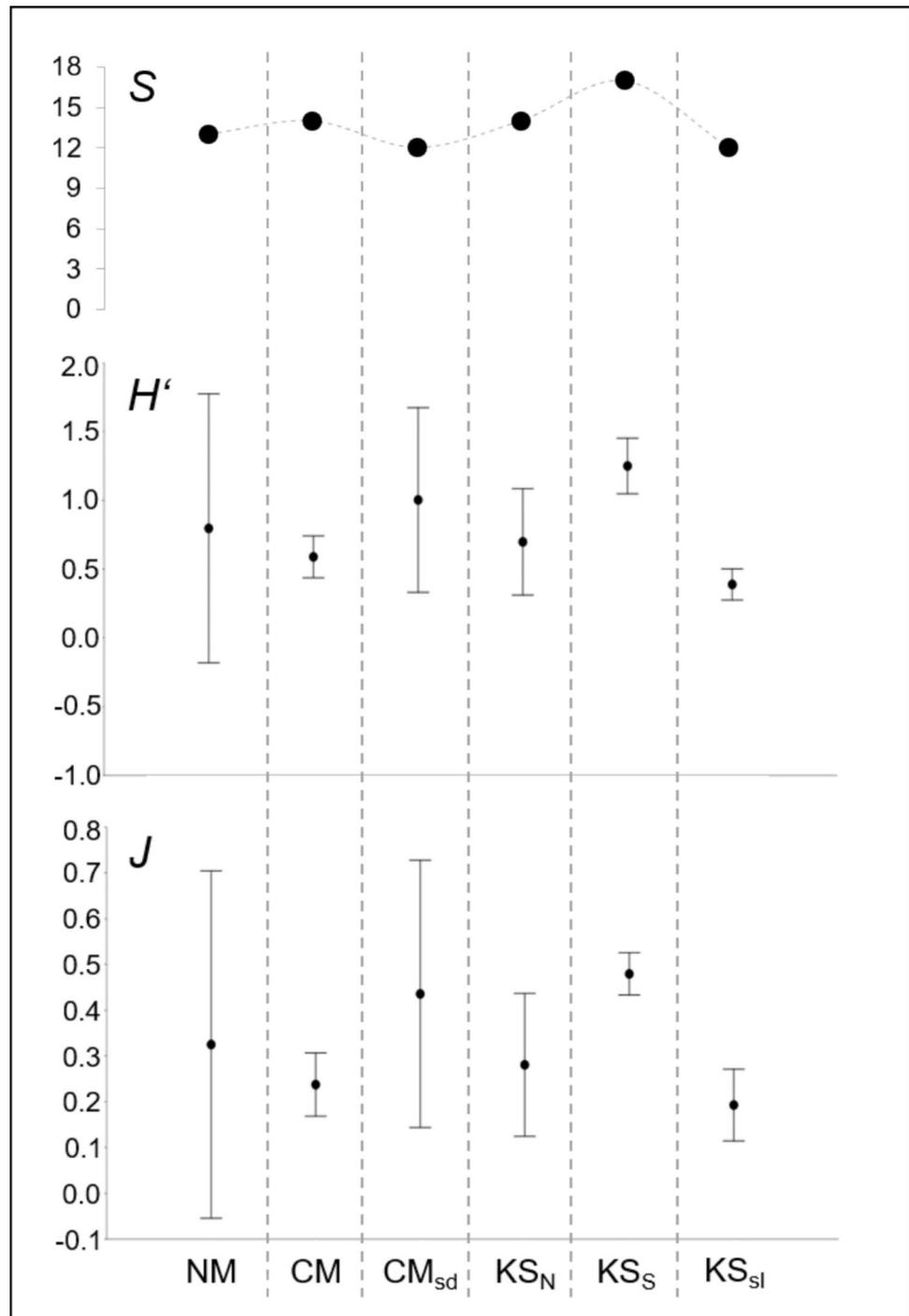
taxon could be detected for Su_A/Su_B and to Su_B/Su_C, respectively (Fig. 9A). This showed that, apart from the ubiquitous taxa, there appears to be a strict faunistic separation between the substratum of (predominantly) sponge needles and polychaete tubes (STM, Su_A) and the underlying bottom sediment (Su_B). This separation is made even clearer by the exclusive occurrence of single taxa in the two substrates (Fig. 9A). In contrast, Su_A and Su_C show a comparatively

large number of common taxa ($S = 6$, Fig. 9A). A look at the corresponding abundance values of the different substrata seems to basically confirm the picture drawn above (Table 6). All three substrate types differ clearly from each other. It is noticeable that most taxa were found in the substrate Su_A, followed by those of Su_C.

In contrast, the highest abundance values were detected in Su_C (Fig. 9B). Substrate Su_B is clearly inferior in both

Table 5 Results of a comparative diversity analysis of the stations sampled during cruise P101 of RV POLARSTERN (2016) along the High-Arctic Langseth Ridge

Area	NM			CM			CM$_{sd}$			KS$_N$		KS$_S$			KS$_{sl}$		
Station	194	195	196	152	153	205	210	211	212	123	125	102	103	104	218	219	220
S	12	9	12	11	13	12	10	10	10	12	12	16	13	12	7	9	7
N	3786	9932	4216	8005	4018	7460	4585	2718	4674	4887	5627	4025	7894	5049	5499	7546	4248
H'	1.263	0.269	0.8563	0.6548	0.6076	0.5034	0.6073	1.215	1.187	0.8374	0.5577	1.363	1.160	1.228	0.3922	0.3279	0.4435
J	0.5081	0.1224	0.3446	0.2731	0.2369	0.2026	0.2638	0.5276	0.5156	0.337	0.2244	0.4915	0.4522	0.4944	0.2015	0.1492	0.2279

Given are: the number of reported taxa S, the number of collected specimens N, and the calculated diversity values of Shannon's H' and Pielou's Evenness J

NM Northern Mount, *CM* Central Mount, *CM$_{sd}$* Central Mount saddle, *KS$_N$*, *KS$_S$* northern and southern peak of Karasik Seamount, *KS$_{sl}$* southern slope at Karasik Seamount

aspects: the fewest taxa and the lowest abundances were consistently found there (Table 6, Fig. 9B). Looking at the six dominant taxa, it can be seen that Nematoda were found most frequently on all substrate types, followed by Copepoda. However, differences emerge concerning the taxa less dominant to Nematoda and Copepoda: in Su$_A$, Tardigrada are the third most common taxon after Nematoda and Copepoda, followed by Annelida, Gastrotricha and Acari. In Su$_B$, on the other hand, the Annelida move up to the third position, whilst the Tardigrada follow in fourth place. As in Su$_A$, Acari are also the sixth most common taxon in Su$_B$; they are, however, overtaken by the Tantulocarida, which for their part are not among the dominant taxa in either Su$_A$ or Su$_C$ but have pushed the Gastrotricha completely aside in Su$_B$ (Table 6, Fig. 9B).

In Su$_C$, as in Su$_B$, the Annelida are the third most common taxon. However, they are followed here by the Acari, which displace the Tardigrada in fifth place. Gastrotricha take sixth place in Su$_C$. This substrate type has the highest abundance values among the Nematoda, which, however, decrease significantly for the Copepoda. These make up just 9.4% of the mean abundance of Nematoda, whereas in Su$_A$ they reach 42.8%. This gave us the following picture: Su$_A$ and Su$_C$ are much more similar in terms of the number S of taxa and the abundance values than with Su$_B$. In addition to the much lower number of taxa and the lower abundance values, Su$_B$ is also characterised by the fact that it is the only substrate type to harbour the Cumacea (Fig. 9A), and the Tantulocarida are among the six dominant taxa (Table 6).

Similarity analyses

As with the geographical comparison, the stations do not form clear groups in relation to the different substrates using the Bray–Curtis index on absolute abundance values (Fig. 10A). It is nevertheless recognisable that the Su$_A$ stations and those from the Su$_C$ are closer to each other; stations 123 A and 125 A are even placed in the middle of the Su$_C$ cluster, whereas their corresponding Su$_B$ stations (123B, 125B, Fig. 10A) are located far away. This drastic separation between the Su$_A$ and Su$_B$ stations is also shown as an example at station 104 (A, B) in Fig. 10A.

An ANOSIM ($r_w = 76.95$; $r_b = 165.9$; $R = 0.6445$, $p = 0.0001$) confirms the significance of the observed grouping of the stations with regard to the different substrates.

As was the case with the geographical comparison, the second similarity analysis using the Cosine Similarity (Fig. 10B) indicates qualitative differences in the distribution of the most dominant taxa. On the one hand, the substrata are also roughly assigned to each other according to their different characteristics, and here too, stations 123 A and 125 A are in the centre of the Su$_C$ cluster. On the other hand, however, the proximity of the Su$_A$ to the Su$_C$ cluster
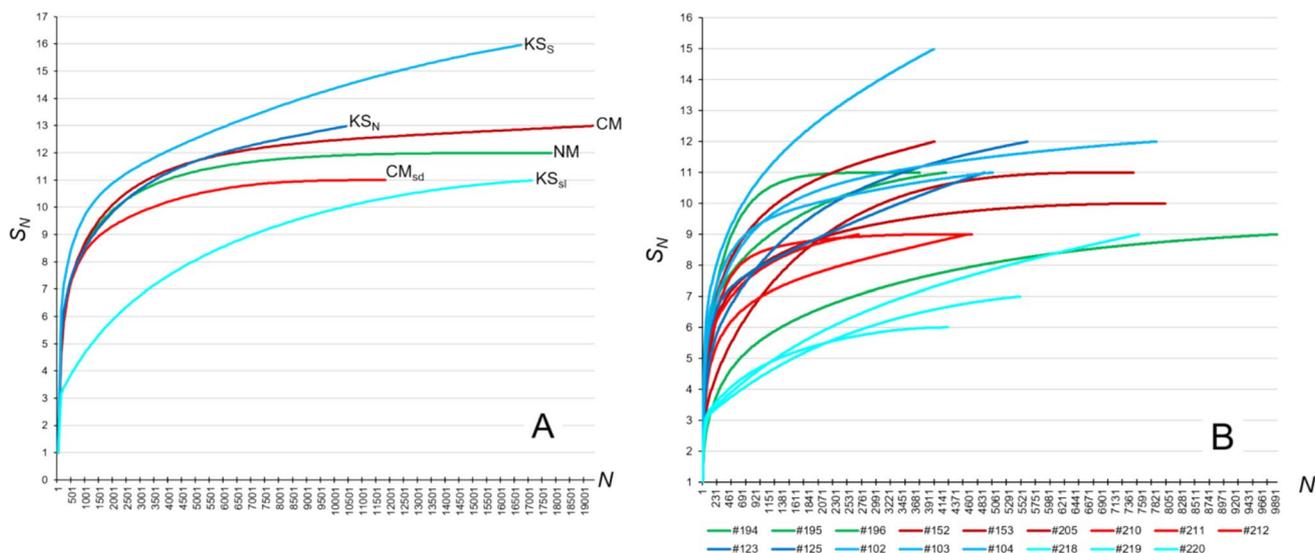
Fig. 8 Rarefaction curves estimated from the meiobenthic material sampled during cruise P101 of RV POLARSTERN (2016) along the High-Arctic Langseth Ridge. **A** Curves interpolated for the different areas, **B** Curves interpolated for the single stations. N specimen num-ber, *NM* Northern Mount, *CM* Central Mount, CM_{sd} Central Mount saddle, KS_N, KS_S northern and southern peak of Karasik Seamount, KS_{sl} southern slope at Karasik Seamount, S_N interpolated number of taxa at a given N
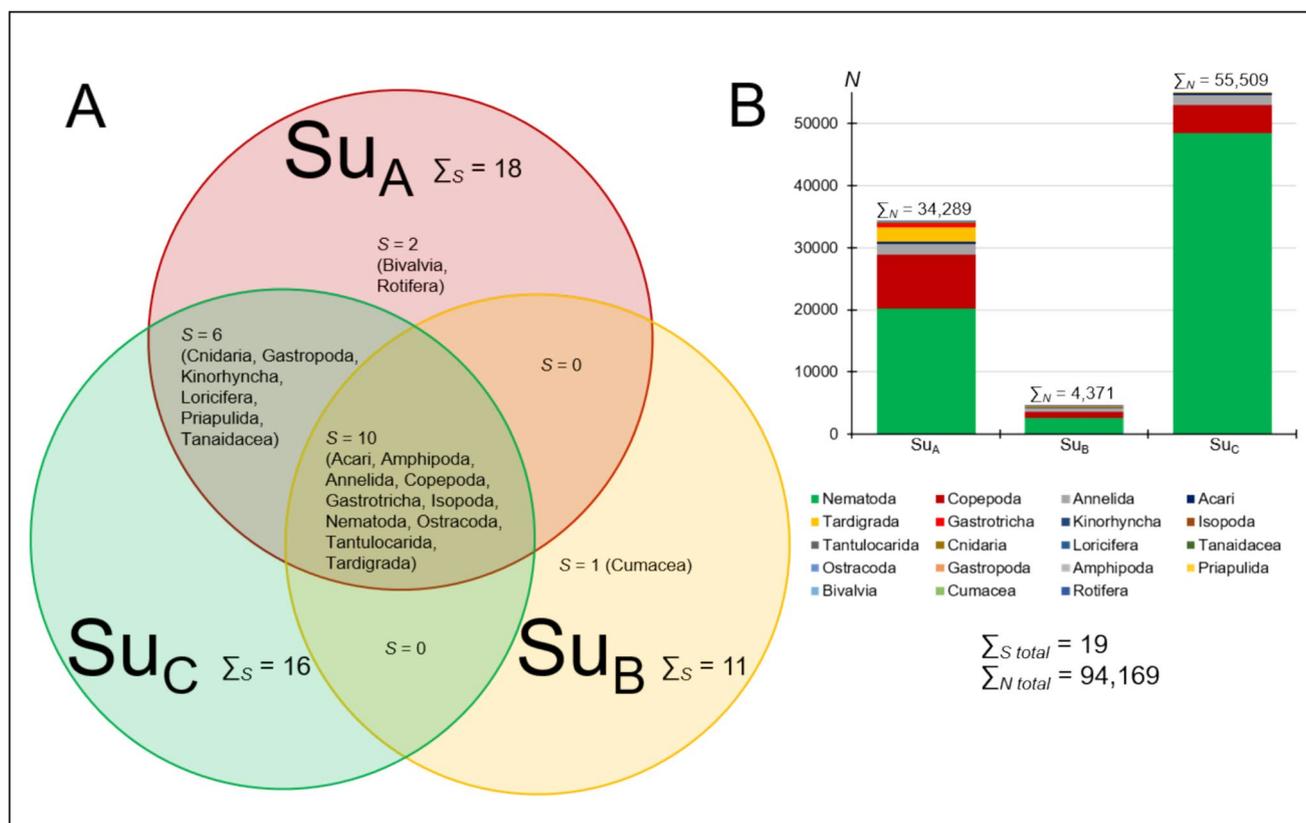
Fig. 9 Distribution of the collected meiobenthic major taxa across the three substrate types, **A** 3-set Venn diagram showing the assignment of the major meiobenthic taxa collected during cruise PS101 of RV POLARTSTERN (2016) along the Langseth Ridge to the respective substrates (Su_A–Su_C), **B** Absolute abundance values N of the major meiobenthic taxa in the different substrates (all cores and hauls per substrate summed)

Table 6 Stations of the meiofauna samples collected during expedition PS101 at the LR, sorted according to the different substrate types

Substrate	Su$_A$								Su$_B$							Su$_C$								
Sample	194A	102A	103A	104A	123A	125A	211A	212A	102B	103B	104B	123B	125B	211B	212B	152C	153C	195C	196C	205C	210C	218C	219C	220C
$\sum N$	3786	3728	6925	4894	3893	5515	1911	3637	297	969	155	994	112	807	1037	8005	4018	9932	4216	7460	4585	5499	7546	4248
Mean N	4,286.13								624.43							6,167.67								
SD	1,493.90								418.13							2,126.71								
S	12	15	12	12	12	12	10	10	9	9	7	7	5	6	9	11	13	9	12	12	10	7	9	7
Most abundant taxa +mean N	Nematoda 2,531.00								Nematoda 366.14							Nematoda 5,379.11								
	Copepoda 1,082.38								Copepoda 136.57							Copepoda 505.89								
	Tardigrada 301.00								Annelida 91.57							Annelida 181.11								
	Annelida 203.25								Tardigrada 30.57							Acari 31.56								
	Gastrotricha 76.13								Tantulocarida 11.29							Tardigrada 29.89								
	Acari 48.38								Acari 9.43							Gastrotricha 15.11								

The different colours correspond to those in Fig. 9

Listed are the sums of the absolute abundances ($\sum N$), the mean values (Mean N) and standard deviations (SD) in the respective substrate type, the taxa number S at the single stations and the six dominant taxa in the corresponding substrate types with their mean abundance values

as revealed by the Bray–Curtis index is not recognisable. Instead, the Su$_B$ stations are closer to those of Su$_C$_i.e. more similar to each other—while the Su$_A$ stations are clearly separated. Moreover, only the Su$_C$ stations cluster close together. Instead, the Su$_A$ and Su$_B$ stations are widely scattered in the ordination plot (Fig. 10B). This constellation does not change even if the two outlier stations 104 A and 104B are omitted in a second iteration (not shown).

An ANOSIM was also carried out here. It confirmed the clear differences between the substrates ($r_b = 157.4$ versus $r_w = 95.96$) but at the same time showed that the values for the stations are widely scattered even within a substrate type ($R = 0.4454$; $p = 0.0001$).

Diversity analyses

The different aspects under which biodiversity can be considered are revealed in the following comparison of the three substrates. If one looks at the number of taxa in the respective substrate types in Fig. 9B, then Su$_A$ with $S = 18$ appears to have the greatest diversity compared to Su$_C$ ($S = 16$) and above all Su$_B$ ($S = 11$). A comparison of the diversity values H' also reveals the greatest taxa richness H' in Su$_A$, but now followed by Su$_B$ (Table 7).

In contrast, Su$_C$ shows only a half as much taxa richness. However, the values vary within the different substrates from station to station. Su$_A$ exhibits the greatest H' fluctuations between the stations (SD = 0.2852), although these are also considerably large in Su$_B$ (SD = 0.1573) and Su$_C$ (SD = 0.1833). Regarding the evenness, the distribution of individuals among the taxa is most even in Su$_B$ ($J_{mean} = 0.536$), followed by Su$_A$ ($J_{mean} = 0.4430$). Su$_C$, on the other hand, has an Evenness value ($J_{mean} = 0.2247$) that is only about half as high (Table 7). The determination of the relative abundance of the two clearly dominant taxa Nematoda and Copepoda confirms this: in Su$_B$, they together reach a relative abundance of only 76.75%, but in Su$_A$ already 84.30% and in Su$_C$ even 95.42%.

A graphical comparison of the values determined for the three substrates also clearly shows the differences between them (Fig. 11). The fact that the Q1 and Q3 quartiles coincide with the maximum and minimum values is due to the moderate amount of data available.

The similarity and diversity analysis of the three substrates led to the conclusion that the three substrate types Su$_A$, Su$_B$ and Su$_C$ do not harbour a uniform overarching meiofauna association, despite observable partial similarities in taxa composition, abundance and single diversity values. Instead, the substrates could be quite well differentiated from each other on the basis of the faunistic data. Hypothesis $H_0 2$ was therefore rejected. We have to keep in mind, though, that especially the comparison of the abundance values between the different substrate types may be biassed by the varying

thickness of the STM/Su$_A$. The thicker the Su$_A$ is, the higher the absolute values probably are. However, we think if Su$_A$ could have been sampled quantitatively, the difference between the three substrate types would even show up more obvious than less. It should also be considered that Su$_A$ and Su$_C$ are in direct contact with the water body above them. This exposes them to comparable inputs of nutrients, oxygen and other environmental variables. This circumstance may explain, at least in part, the greater similarity between Su$_A$ and Su$_C$ in terms of taxon composition and diversity on the one hand, and the difference to Su$_B$ on the other, which is not directly exposed to the environmental influences mentioned; in fact, future comparisons of this kind should consider that the Su$_B$ horizon may need to be compared with a depth layer of Su$_C$ that corresponds to the thickness of the Su$_A$ above Su$_B$. Górska et al. (2014) were able to show for taxonomic diversity that sediment depth plays an essential role in the establishment of meiofauna and nematode communities; these are also more similar at different water depths than communities of shallower sediment layers at the same water depth. This observation was also confirmed by Schnier and Hasemann (2026) with regard to functional diversity.

Comparison with the meiofauna communities of other seamounts

The Langseth Ridge is the northernmost complex of submarine elevations ever investigated for meiofauna so far (Fig. 12). It therefore seemed obvious to compare the meiobenthic community found there with those of other seamounts. For this comparison, we had to make certain compromises by not including all taxa listed in the different studies. For example, we combined the taxa Polychaeta and Oligochaeta into the Annelida because both taxa are not always differentiated (cf. George 2022). We also did not include representatives of the Protista (e.g. Ciliata, Foraminifera) because they are not listed in every comparative study. Finally, taxonomic uncertainties also had to be considered: some organisms could not be clearly assigned to an animal group. The updated list of meiobenthic major taxa found on seamounts and oceanic islands (Fig. 12) therefore excludes uncertain groups. We have added our new data to the comprehensive list of major meiobenthic taxa on seamounts and islands compiled by George (2022). In addition to the findings made at the LR (present study), we were also able to add those from the Senghor seamount (Cape Verde archipelago, subtropical east Atlantic (Kieneke et al. 2025). To date, 21 seamounts and oceanic islands in the Atlantic, the Mediterranean and the Arctic Ocean have been sampled for meiobenthos, and twelve of them (Fig. 12: red data) have already been processed and provide at least qualitative data on the composition at major taxa level; samples of nine expeditions are still awaiting processing and determination of meiofauna major taxa (Fig. 12: blue data).

An initial comparison of the 12 analysed seamounts and island shelves reveals that there are already differences at the major taxa level. Of the 27 major taxa analysed, only seven (25.90%) have been reported from all elevations, i.e. in an area from the Cape Verde Islands/Mid-Atlantic to the North Pole and the eastern Mediterranean. This contrasts with five taxa (Fig. 12: 18.52%) that were only found on a single seamount/island. And more than half of the 27 major taxa ($S = 15$; 55.56%) were found on at least two of the 12 studied marine elevations (Fig. 12). In order to gain a more comprehensive insight into the distribution of meiobenthic major taxa, we have subjected the two most abundant representatives, Nematoda and benthic Copepoda, to a geographical and bathymetric comparison.

We used density values (ind./10 cm^2) obtained from literature data (Gutzmann et al. 2004; Zeppilli et al. 2013; George et al. 2014, 2018, 2021; Richter and George 2019; George 2022; Kieneke et al. 2025) as well as our own (not yet published) datasets from expeditions that explored not only seamounts (Anaximenes seamount) but also the southeastern Atlantic deep sea (DIVA 2; see supplement S2). The comparisons served to provide an overview of the density spread of Nematoda and benthic Copepoda across the geographic range of the respective study areas. For this purpose, we grouped the compared expedition data into seven regions, which extend more or less along a latitudinal gradient from the West Antarctic across the Atlantic to the High Arctic, with a swing to the eastern Mediterranean (Fig. 13, small map).

The result of the latitudinal comparison was surprising. As can be seen in Fig. 13, no distinct group of "seamounts and islands" can be distinguished from the deep-sea regions. Instead, deep-sea stations—whether at seamounts or in the deep-sea plains of the Atlantic and Antarctic—have remarkably higher density values than the shallow areas ("turning point" ≤ 312 m, cf. Fig. 14) of the analysed islands and seamounts. This becomes particularly clear at the deep stations of the Condor seamount and along the Langseth Ridge. But even Anaximenes and Eratosthenes seamounts, which are located in the eastern Mediterranean and thus in a less productive marine region (e.g. Kröncke et al. 2003; Lubinevsky et al. 2017), show higher density values at their deep stations than at the shallow ones (Fig. 13, supplement S2). In contrast, the investigated islands of the Azores and the Great Meteor Seamount, which were sampled at water depths of around 300 m, are characterised by much lower densities. These are contrasted again by the very shallow stations (~ 100 m depth) of the Senghor Seamount, which are characterised by high-density values.

If the density values are plotted along an increasing water depth (Fig. 14), the picture becomes even clearer. Here, too,
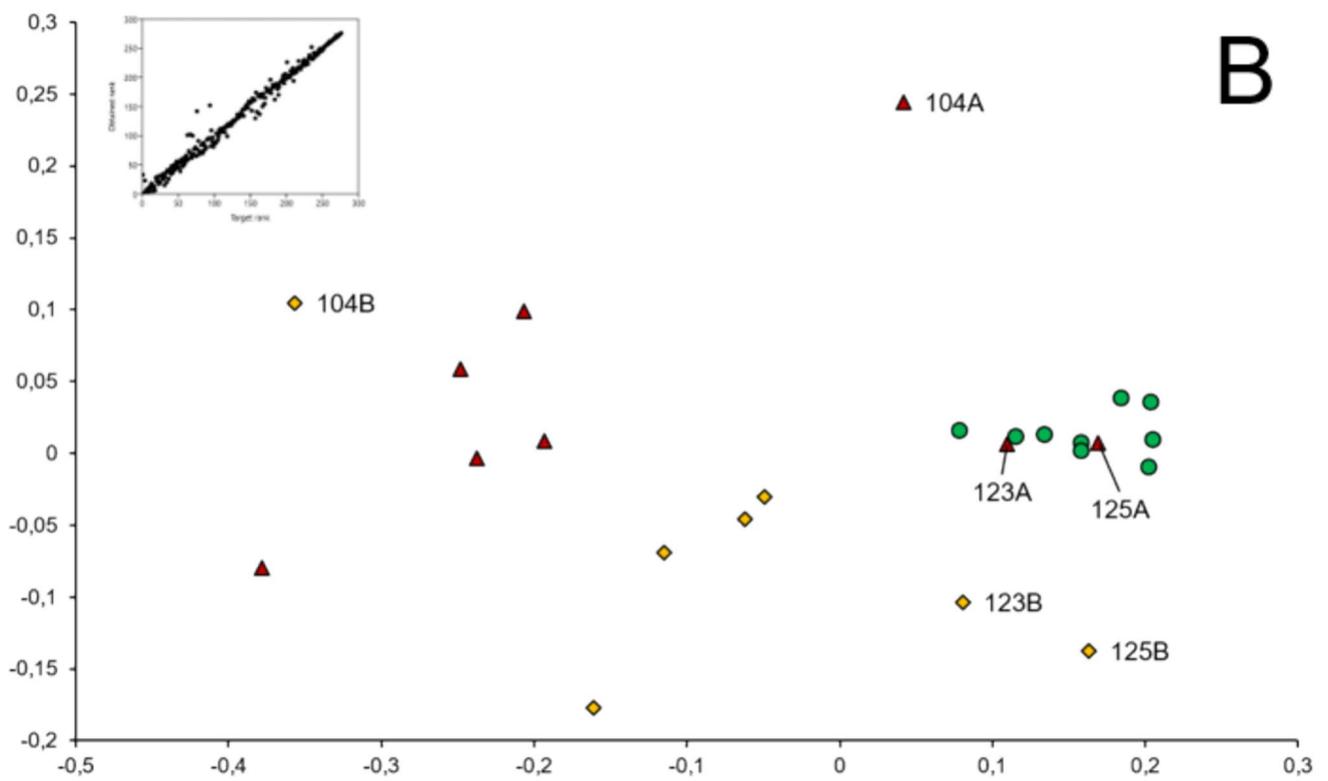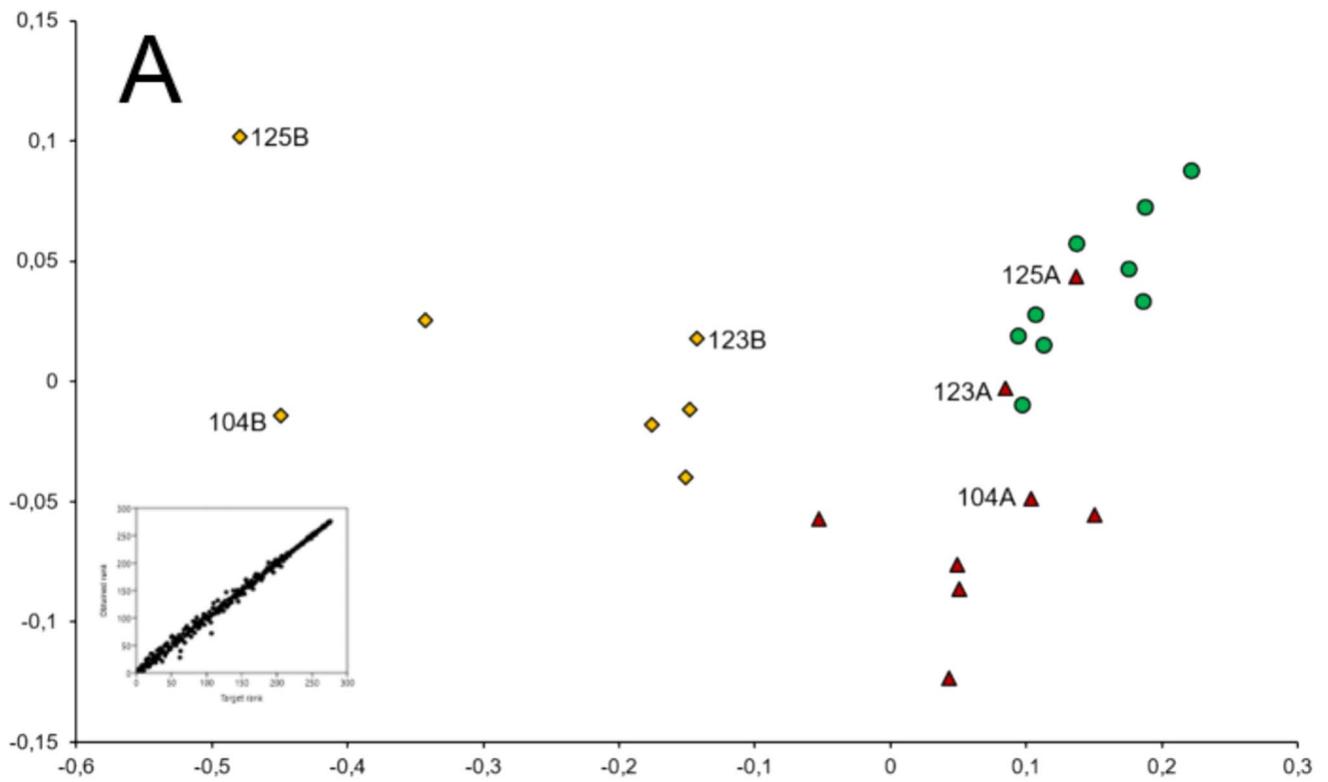
◄**Fig. 10** Ordination plots of a non-metrical Multidimensional Scaling, showing the mutual (dis)similarity of the stations sampled at the Langseth Ridge, according to the composition and absolute abundance of the meiobenthic major taxa found during cruise PS101 of RV POLARSTERN (2016), and according to the different substrate types. **A** Bray–Curtis index, stress = 0.04132. bottom left: Shepard diagram, **B** Cosine Similarity index, stress = 0.06089. Top left: Shepard diagram. Red triangles: Su_A; yellow rhombi: Su_B; green circles: Su_C

the very shallow stations of the Senghor Seamount as well as the summit station of Condor Seamount (~ 200 m depth; corresponding to the deep sublittoral) show high-density values, in particular for the Copepoda. However, the values drop significantly in a range between 200 and about 300 m water depth (= the shallow bathyal) and only reach values below $D = 100$ ind./10 cm^2 for Nematoda and benthic Copepoda (Fig. 14, supplement S2). In contrast, the subsequent deeper bathyal (down to about 4000 m) is characterised by a remarkable variability of density values that reach the highest peak values at depths between 2000 and 4000 m, particularly for the Nematoda.

The benthic Copepoda basically follow the same trend, but the difference between the middle and deep range is not as pronounced as with the Nematoda. In addition, the variability of the density values for copepods only extends to a water depth of around 1500 m and then remains fairly constant up to around 5660 m, i.e. the abyssal. Likewise, the abyssal zone is characterised by relatively uniform, comparatively high-density values for Nematoda (Fig. 14, supplement S2). Against the background of the above comparisons, hypothesis $H_0 3$ can be assessed as follows: at the major taxon level, there are certainly indications of a similarity of the meiofauna communities on different seamounts. Almost 26% of the taxa found were recorded on all the seamounts and islands investigated so far, and a further 18.5% on the vast majority. However, with 55.6%, more than half of all taxa could only be detected sporadically or on a few seamounts, but it cannot be ruled out that the absence of rare taxa in particular may be due to the fact that these rare taxa were simply not recorded during sampling. On the other hand, the studied seamounts and islands show differences in terms of specimen density, as shown in Figs. 13 and 14. Hence, we have both indications for similarities and differences between different seamounts and islands, and $H_0 3$ can neither be refuted nor supported at this point in time. We suspect that analyses on the species level will reveal more significant patterns.

Discussion

$H_0 1$: The meiofauna assemblages of the six sampled areas at the LR do not differ in composition or taxa diversity.

The community-analytical comparison of both the investigated areas (NM, CM, CM_{sd}, KS_N, KS_S, KS_{sl}) and the individual stations led to the acceptance of hypothesis $H_0 1$. Nevertheless, it would have been quite conceivable that at least the investigated summits KS_S, KS_N, CM and NM harbour different meiofaunal communities due to their more or less pronounced geographical isolation. The fact that seamounts such as the Great Meteor Seamount harbour isolated species communities (then called "trapping stones") due to their isolated location, special current conditions and other abiotic features (cf. Gad and Schminke 2004) has also been documented by various authors for meiofaunal representatives (e.g. George and Schminke 2002; Gad 2009; Plum and George 2009; Richter and George 2019). Other studies have concluded that seamounts and islands can also act as stepping stones for meiobenthos (e.g. Gad and Schminke 2004; Büntzow 2011; Packmor et al. 2015; Packmor and Riedl 2016; Packmor and George 2018; Yamasaki et al. 2018), and in turn the vast deep-sea plains could represent barriers against long-distance dispersal by population growth at least for certain taxa such as Gastrotricha and Tardigrada, which would underline a stepping stone function of seamounts and island shelfs (Trokhymchuk and Kieneke 2024).

The findings of 10 of the 19 major meiobenthic taxa on all six elevations, in combination with the consistent dominance of Nematoda, benthic Copepoda, Annelida and Tardigrada at all sites support the assumption of $H_0 1$. Registered differences such as the lower abundance values at CM_{sd} and KS_N (Fig. 3A), varying relative abundances (Fig. 3B) up to individual finds of certain major taxa (Bivalvia, Cumacea, Priapulida, Rotifera; see Table 2), suggest a heterogeneous but nevertheless single meiobenthic community that extends over all investigated summits of the Langseth Ridge. This was confirmed by the comparison of the stations, where neither the similarity nor the diversity analysis showed a clear separation of the areas, but rather a strong mixing of the stations based on the composition of the meiofaunal taxa. We can therefore speak of a heterogeneous meiobenthic "Langseth community". The individual areas, in particular the different summits, correspond to the model of "non-isolated" seamounts arranged in chains presented by Gad and Schminke (2004: 51, Fig. 4). We assume medium to small-scale changes or fluctuations in environmental variables to be the cause of the nevertheless recorded non-uniformity between the areas of the LR. Such are also assumed to be the cause of similarly inhomogeneous meiobenthic communities at other seamounts, both at the major taxa level (George 2022; but also see Zeppilli et al. 2013) and in species-level studies of the Harpacticoida (George et al. 2018; Richter and George 2019).

$H_0 2$: The different substrates studied do not harbour different meiobenthic communities, neither in terms of taxa composition nor diversity.

Table 7 Number S of taxa found in the substrata Su_A, Su_B and Su_C and the corresponding calculated diversity values H' and J

Substrate	Su_A									
Station	194A	102A	103A	104A	123A	125A	211A	212A		
S	12	15	12	12	12	12	10	10	Mean	SD
H'	1.263	1.374	1.149	1.22	0.7624	0.5463	1.271	1.142	1.091	0.2852
J	0.5081	0.5074	0.4625	0.4912	0.3068	0.2198	0.5519	0.496	0.443	0.116
Substrate	Su_B									
Station	102B	103B	104B	123B	125B	211B	212B			
S	9	9	7	7	5	6	9	Mean	SD	
H'	1.053	1.111	1.24	1.01	0.7762	1.022	1.23	1.063	0.1573	
J	0.4794	0.5058	0.6373	0.5191	0.4823	0.5707	0.5597	0.536	0.0567	
Substrate	Su_C									
Station	152C	153C	195C	196C	205C	210C	218C	219C	220C	
S	11	13	9	12	12	10	7	9	7	Mean	SD
H'	0.6548	0.6076	0.269	0.8563	0.5034	0.6073	0.3922	0.328	0.4435	0.518	0.1833
J	0.2731	0.2369	0.1224	0.3446	0.2026	0.2638	0.2015	0.149	0.2279	0.2247	0.0667

The right-hand columns show the respective average values

Sediment structure plays a very important role in the colonisation of habitats by meiobenthos (e.g. Coull 1988; Giere 2009). Its representatives (i.e. species) often not only developed special morphological and anatomical adaptations to the substrate type they inhabit (Coull 1988) but are even able to "recognise" the preferred substrate with all its properties (grain and pore size, penetration by or overgrowth with algae and bacteria) and colonise it in a very targeted manner (Giere 2009 and citations therein).

At the Langseth Ridge, we had to deal with the three substrate types Su_A, Su_B and Su_C. Su_B and Su_C stand for muddy, compact sediment, as is often found in the deep sea. Su_A, on the other hand, is a several cm-thick layer above Su_B consisting mainly of sponge needles and polychaete tubes and called the spicule-tube-mat, STM (see introduction and Morganti et al. 2022), while Su_C is in direct contact with the overlying water column.

Almost half of the 19 major taxa analysed were found in all substrate types. At this taxonomic level, it can be stated that these 10 taxa show no particular preference for one substrate type. However, the situation is different with regard to the 6 taxa that were found in both Su_A and Su_C, but not in Su_B. As they were found on exposed muddy substrate (Su_C), it can be assumed that this substrate also offers them good habitat conditions here at the Langseth Ridge. However, at those sites where the muddy substrate (Su_B) is covered by a complex-structured layer of STM (Su_A), the taxa obviously show a clear preference for this three-dimensional, duct- and pore-rich biogenic substrate, as they are completely absent in the underlying sediment (Su_B). This fact leads us to the conclusion that representatives of the meiofauna, even if they

are regularly found on muddy substrate (e.g. Coull 1988; Giere 2009; see also Schmidt-Rhaesa 2020), prefer a three-dimensionally and diversely structured layer, as can be seen from the six common taxa of Su_A and Su_C, which, however, could not be detected in the Su_B underlying Su_A. With regard to the fact that Su_A and Su_C are directly connected to the overlying water body, while Su_B lies below Su_A with varying layer thicknesses, it should be noted, despite the recommendation made above to extend comparisons to comparable sediment depths in future studies, that such comparisons do not always appear to be meaningful. In soils where Su_B lies beneath a Su_A layer that is > 5 cm thick (in the present study, up to approx. 15 cm in some cases), a comparison with sediment from Su_C at the same depth (> 5 cm) is unlikely to be promising. Studies of the past decades demonstrate that meiobenthos, especially in muddy compact sediments, is usually found at depths of up to approximately 2–5 cm (e.g. Coull 1988; Giere 2009), whereas it is very rarely found at depths below 6–8 cm (e.g. Somerfield et al. 2005).

As far as the exclusive taxa of Su_A and Su_B are concerned (Bivalvia and Rotifera, respectively, Cumacea, Fig. 9A), we are not able to make any assumptions about possible substrate preferences. The low yield of individuals of these taxa (Table 2) rather indicates that their absence on the other substrate types could well be an artefact of the sampling: Because they are rare, they had simply not been recorded based on the low number of replicates.

$H_0 3$: The meiofaunal assemblages at the LR do not differ from those of other seamounts.

The faunistic comparison of different regions on the basis of taxonomically higher categories than the species

Fig. 11 Box-whisker plots with the mean *H'* and *J* values of the Langseth Ridge stations, assigned to the three substrate types Su_A, Su_B and Su_C. Shown are the arithmetic mean, the maxima and minima, and (red lines) the quartiles Q1 (25% of all measured data below that value) and Q3 (75% of all measured data below that value)
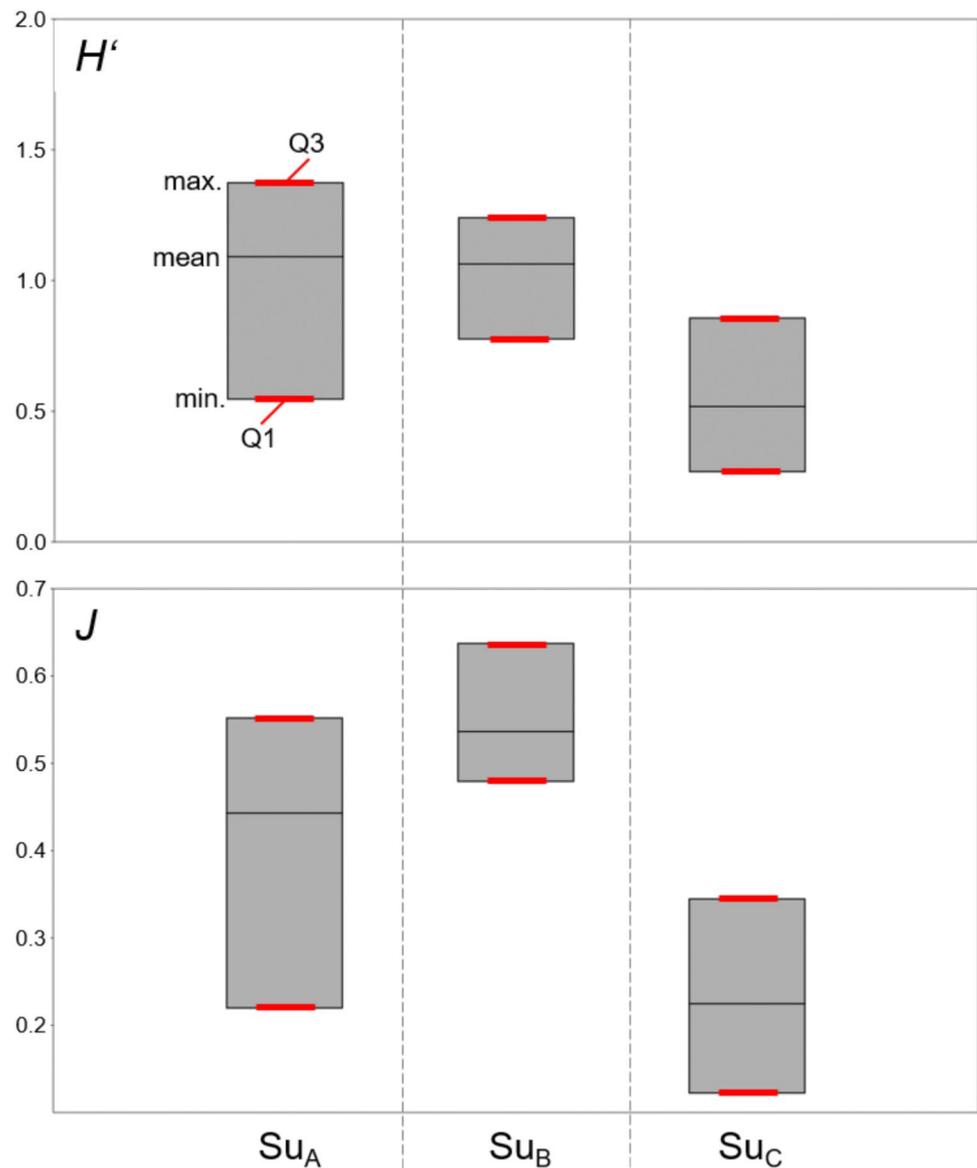
level always harbours the risk of generalisation, because species-specific interactions and thus faunistic differences may be blurred at a higher taxonomic level (e.g. George 1999; Richter and George 2019 and references therein). On the other hand, ecological comparisons at a higher taxonomic level may already provide information on distribution patterns and enable comparative community analyses (e.g. Heip et al. 1988; Herman 1989; Herman and Dahms 1992; Chen et al. 1999). Some studies of the meiobenthos of seamounts and oceanic islands have already undertaken an inventory of the major taxa (e.g. George and Schminke 2002; Büntzow 2011; George 2013, 2022; Zeppilli et al. 2013; George et al. 2021), although the actual aim of several studies was to investigate only one or a few taxa at the species level (e.g. Clausen 2004; Gad 2004a, b, 2009; Hansen 2005; Heiner 2005; Koller and George 2011;

George et al. 2018; Packmor and George 2018; Richter and George 2019).

Since the review by George (2013), the number of seamounts surveyed in the Atlantic for major meiobenthic taxa has increased from four to seven: studies of the Great Meteor Seamount, Seine Seamount, Sedlo Seamount and the Faroe Bank were expanded to include the Condor Seamount (Zeppilli et al. 2013), Senghor Seamount (Kieneke et al. 2025) and the peaks of the Langseth Ridge (current study). In addition, the processing of the two eastern Mediterranean seamounts Anaximenes (cf. George et al. 2018) and Eratosthenes (George 2022) as well as the Azores islands Flores, Terceira and Santa Maria (George et al. 2021) provided data from five further oceanic elevations.

It is noteworthy that since the comparisons of George (2013, 2022) and despite the evaluation of the added

Seamounts and islands sampled and further evaluated for meiobenthic major taxa:

1. Great Meteor Seamount GMS (1998, 2010)
2. Princess Alice Bank PAB (2018)
3. Flores Island Flo (2018)
4. Condor Semount CoS (2010)
5. Terceira Island Ter (2018)
6. Sedlo Seamount SedS (2003)
7. Formigas Bank FoB (2018)
8. Santa Maria Island StM (2018)
9. Madeira Island Mad (2012, 2014)
10. Porto Santo Island PoS (2012, 2014)
11. Desertas Islands Des (2014)
12. Seine Seamount SeiS (2003)
13. Ampère Seamount AmS (2010)
14. Anaximenes Seamount AnaS (2006)
15. Eratosthenes Seamount EraS (2009/2010)
16. Langseth Ridge LR (2016)
17. Senghor Seamount SenS (2009)
18. Josephine Bank JoB (2021)
19. Faroer Bank FaB (1989-2001)
20. Hyères Seamount (HyS) (2009)
21. Irving Seamount (2009)

| No.	Major taxon	Atlantic									Med.		Arct.	No. elev.	S/no. elev.
		GMS	Flo	CoS	Ter	SedS	StM	SeiS	SenS	FaB	AnaS	EraS	LR		
1	Kinorhyncha														
2	Loricifera														
3	Nematoda														
4	Ostracoda													12	7 (25.9%)
5	Tardigrada														
6	Acari														
7	Harpacticoida														
8	Isopoda													11	1 (3.70%)
9	Gastrotricha													10	2 (7.41%)
10	Annelida														
11	Bivalvia													9	2 (7.41%)
12	Tanaidacea														
13	Tantulocarida													8	2 (7.41%)
14	Rotifera														
15	Amphipoda													7	1 (3.70%)
16	Priapulida													5	2 (7.41%)
17	Gastropoda														
18	Cnidaria													4	2 (7.41%)
19	Sipuncula														
20	Cumacea													3	1 (3.70)
21	Pantopoda													2	2 (7.41%)
22	Turbellaria														
23	Bryozoa														
24	Entoprocta														
25	Leptostraca													1	5 (18.52%)
26	Echiura														
27	Solenogastres														
	S	26	13	16	14	14	10	15	17	14	17	15	19		
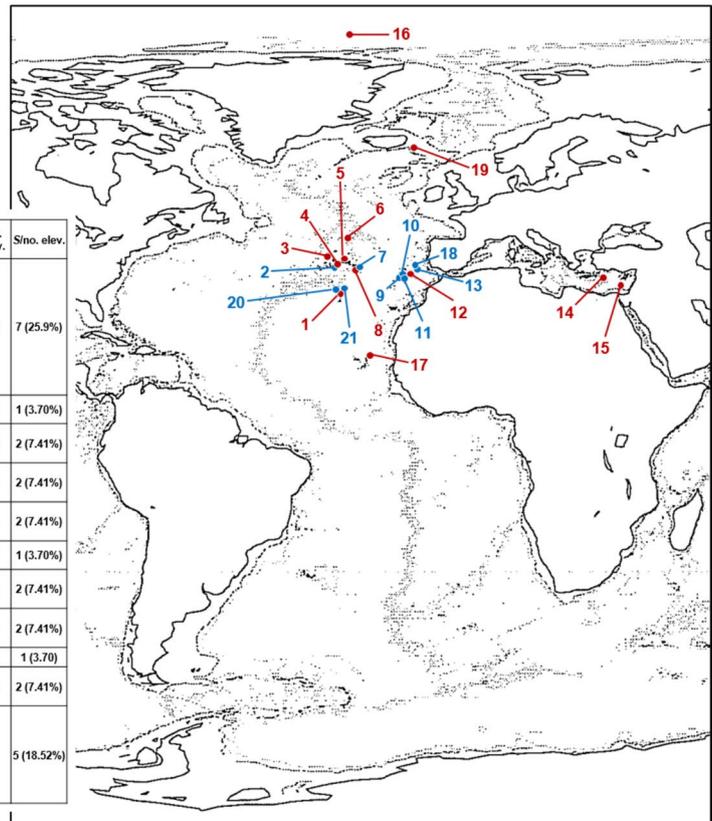
Fig. 12 Map showing the position of the 21 seamounts and oceanic islands sampled to date in the Atlantic, Mediterranean and Arctic (red and blue sites) and those 12 that have so far been surveyed for major meiobenthic taxa (red sites). The years behind the left-hand surveys indicate the year/time frame of sampling. The table shows the 27 major taxa and their occurrence at the studied seamounts/islands. *No. elev.* number of colonised (sub)marine elevations, *S/no. elev.* number of major taxa found on the respective (sub)marine elevations

seamount and island data, the number of meiobenthic major taxa detected has remained almost unchanged. George (2013) had recorded 25 taxa (actually 26, but Oligochaeta and Polychaeta are united as Annelida in George (2022) and here). Echiura and Priapulida are missing in George's (2013) list; Echiura were later recorded at Condor Seamount (Zeppilli et al. 2013), and meiobenthic Priapulida both at Eratosthenes Seamount (George 2022) as well as at the Anaximenes Seamount (present contribution) and the Azores islands Flores and Terceira (George et al. 2021).

In addition to the seven taxa that were found on all (sub)marine elevations (Fig. 12), there are at least seven others that were not found everywhere but were found on most seamounts/islands along the entire latitudinal gradient. Here, we assume that the absence of those seven (or more) taxa on single islands or peaks is rather an artefact of the sampling or the subsequent sorting. In our view, it simply seems more plausible to assume that, e.g. the Isopoda, which have not yet been documented on the Faroe Bank (cf. George 2013), have either been overlooked or simply not considered, rather than actually not occurring there (Fig. 12), and the same applies to other major taxa such as Gastrotricha, Annelida,

Bivalvia and Tanaidacea even on a suprageneric level within a major taxon. For instance, Bartsch (2003) proved a wide distribution of representatives of the Halacaridae (Acari) found on the GMB, and Clausen (2004) was able to confirm a clear proximity to communities of the Mediterranean and the English Channel for the Macrodasyida (Gastrotricha) of the Faroe Islands. Gad (2009) showed a much wider distribution of the Draconematidae (Nematoda) of the GMB than originally assumed, and Packmor et al. (2015), George et al. (2018), Packmor and George (2018) as well as Richter and George (2019) found only minor differences in the Harpacticoida and Canuelloida communities (at supraspecific level) of the seamounts, respectively, islands they compared (i.e. Madeira, Porto Santo, GMB). At the genus level of Gastrotricha, there is also a great overlap between the Faroe Bank, São Miguel (Azores) and Lanzarote (Canary Islands) in both, Macrodasyida and Paucitubulatina (Clausen 2004; Araujo and Hochberg 2021; Martínez et al. 2019; Todaro et al. 2019; reviewed in Trokhymchuk and Kieneke 2024). Even at the species level, such matches occur, as impressively demonstrated for the Harpacticoida by Büntzow (2011), Packmor and George (2018), Packmor and Riedl (2016) and
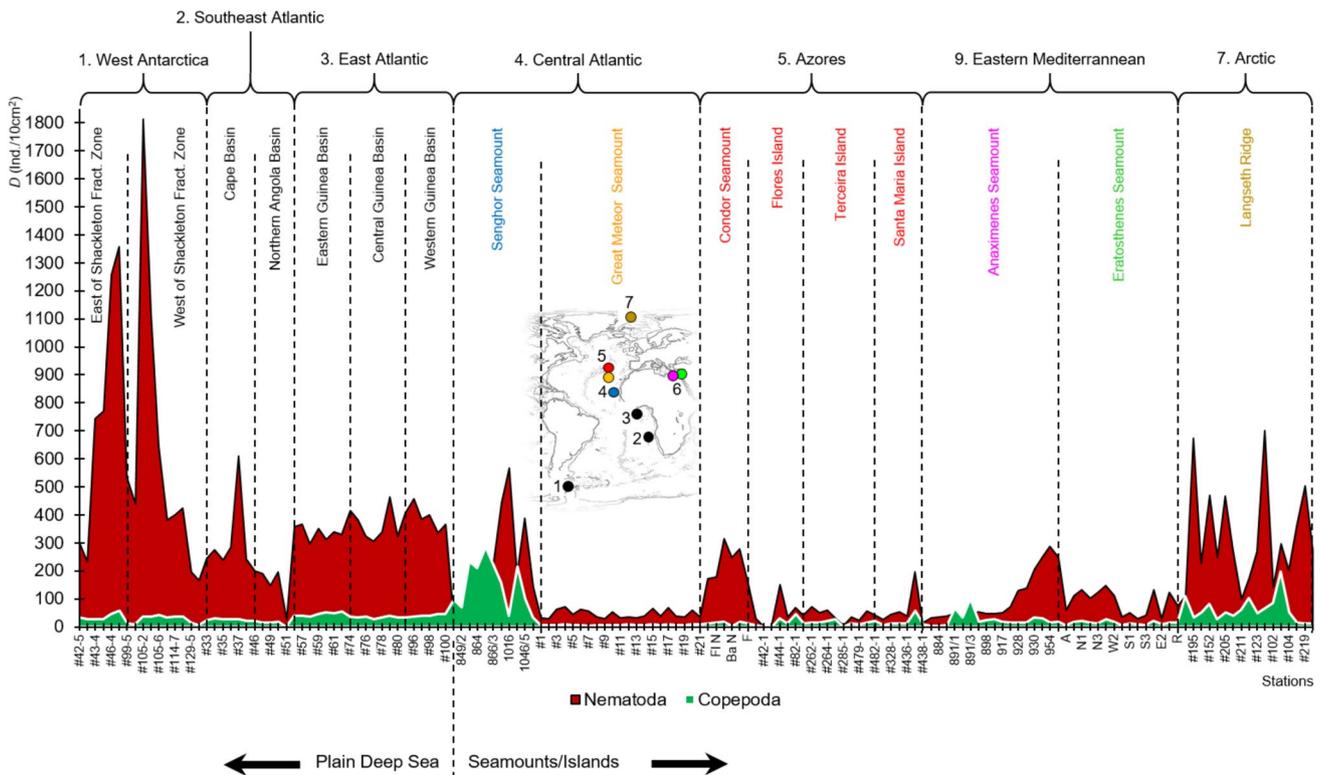
Fig. 13 Densities (ind./10 cm.²) of Nematoda (in red) and benthic Copepoda (in green), plotted along a latitudinal gradient, independent of depth. The seven investigated regions are shown in the small map (for detailed values see supplement S2)
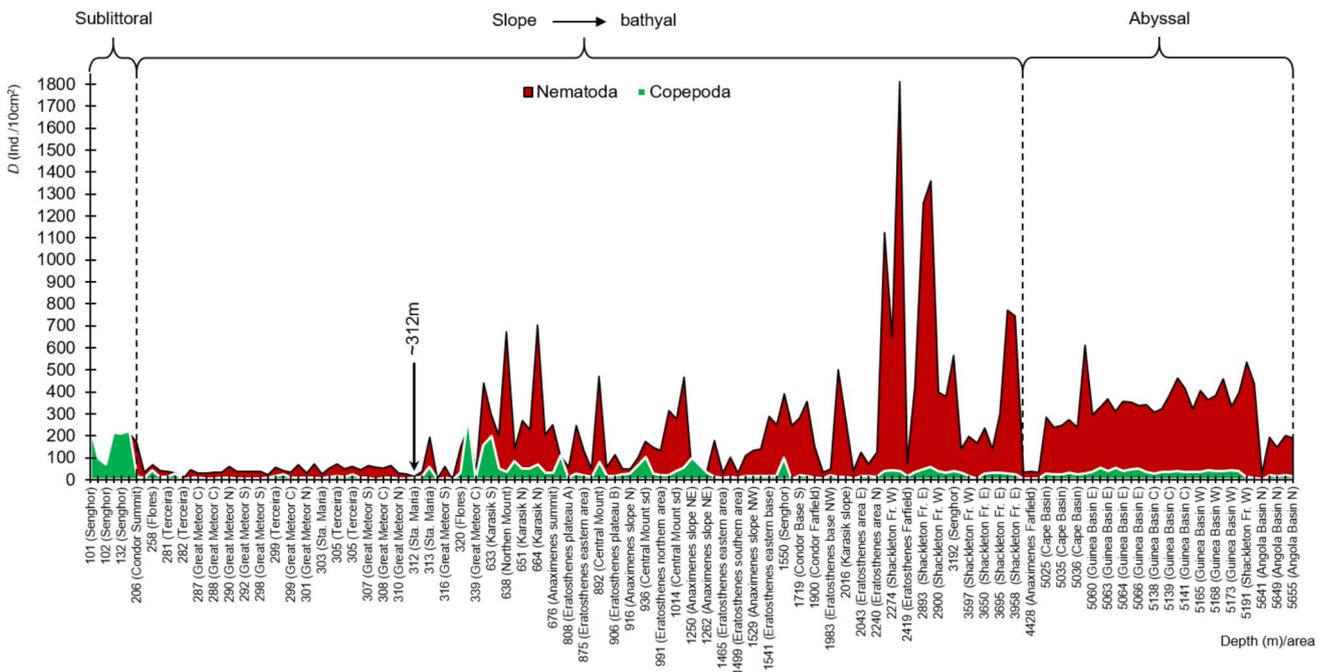
Fig. 14 Densities (ind./10 cm.²) of Nematoda (in red) and Copepoda (in green) plotted along a bathymetrical gradient with added geographic locations. The densities are grouped to three depth ranges (shallow→deep). (At Senghor Seamount, values for Nematoda are lower than those for Copepoda; for detailed values see supplement S2)

George et al. (2018); Clausen (2004) confirmed it for various Gastrotricha species and Yamasaki et al. (2019) for representatives of the Kinorhyncha. All of the aforementioned examples of a wide distribution of meiobenthos representatives on seamounts and islands suggest a rather pronounced faunistic similarity between seamounts and islands, at least in the Atlantic-Mediterranean region, and this at the level of major taxa, families, genera and sometimes even species. In contrast, however, the communities on seamounts and islands themselves are apparently very unevenly structured. Instead of uniform, regularly structured communities, the mostly very large submarine mountains or mountain groups harbour somewhat heterogeneously structured assemblages whose members are distributed across the entire area, but in a very patchy manner (cf. Zeppilli et al. 2013; George 2022). The reasons for this may lie in the likewise non-uniform occurrence of medium- to small-scale (a)biotic variables, such as sediment composition (grain size distribution, sand/mud ratio, flow conditions, increased localised input or localised accumulations of organic material, etc.; e.g. White et al. 2007; Zeppilli et al. 2013; Packmor and George 2018; Tojeira et al. 2025) or, as in the case of the Langseth Ridge investigated here, the partial covering of the actual sediment layer with a complex-structured, biogenic layer of macro- and megafaunal debris. This very heterogeneous structure of a single large community can even be demonstrated at the species level, as was done at the Anaximenes Seamount and the Great Meteor Seamount for the benthic copepods (George et al. 2018; Richter and George 2019). And this in turn could mean that very rare taxa such as Bryozoa, Entoprocta, Leptostraca, Echiura and Solenogastres are simply not detected, although they do occur at the site. The fact that Bivalvia, Rotifera and Cumacea were only found with one and two individuals, respectively, at the Langseth Ridge speaks in favour of this assumption.

However, it could also be that the rare findings of Bryozoa, Entoprocta, Leptostraca, Echiura and Solenogastres, each of which has so far only been found on one seamount (Fig. 12), indicate that their distribution is actually very limited. Bryozoa, Entoprocta and Leptostraca are known exclusively from the Great Meteor Seamount (George and Schminke 2002); Echiura in turn have only been found at the Condor Seamount (Zeppilli et al. 2013), and Solenogastres only at the Sedlo Seamount (Büntzow 2011). The Pantopoda could also have a restricted distribution area along seamounts and islands, as they have only been found at the Great Meteor Seamount (George and Schminke 2002) and the relatively nearby Sedlo Seamount (Büntzow 2011). Other taxa, on the other hand, allow the assumption of a wide distribution on submarine oceanic elevations, although they too have only been found on a few islands or seamounts so far. The distribution area of Cumacea, Sipuncula, Turbellaria and others, for instance, extends very disjunctively

along the entire latitudinal gradient analysed in the current paper, or at least along large parts of it (Fig. 12). We therefore assume that in their case the artefact of inadequate sampling or processing leads to the incomplete coverage. In our opinion, the results of Zeppilli et al. (2013) clearly show that this can even be the case on individual seamounts. In their investigations on Condor Seamount, the authors found Ostracoda only on the summit and on the southern slope of the mount, Isopoda only on the summit and the southern base, Kinorhyncha only on the southern slope and Cumacea only on the northern flank and at Farfield Station. These were contrasted by the abundant taxa Nematoda, Copepoda, Polychaeta and Acari, which were found everywhere (but also the rather rare Loricifera, cf. Zeppilli et al 2013). The even rarer taxa Tanaidacea, Gastropoda, Echiurida and Bivalvia were restricted to only one area each.

Nonetheless, the fact that the data from Zeppilli et al. (2013) were obtained from only two hauls at each of the sites and that only two MUC cores per haul were analysed faunistically raises concerns that these studies are subject to a strong sampling artefact. It can be assumed that a more intensive sampling at the Condor Seamount would have recognised the distribution of the corresponding major taxa as much more uniform and also more wide-ranging, like in the current study of the Langseth Ridge.

The purely qualitative inventory of major meiobenthic taxa is therefore not sufficient to clearly answer hypothesis H_03. There is some evidence to suggest that further sampling at sites where various taxa have so far been noted as "absent" will probably detect these taxa there. In this context, one also needs to consider that major taxa were mostly recorded qualitatively at the respective sites, and this by using different devices, from the multicorer to the van Veen and the Henning grab, the box corer and different sledges and trawls (cf. George and Schminke 2002; George 2013 and references therein, 2022; Zeppilli et al. 2013; George et al. 2018, 2021; Richter and George 2019). A direct comparison can therefore only be made with caution, and a number of major taxa—especially those that are rare anyway—may simply not have been recorded yet. It is also quite possible that rare taxa in particular were overlooked during subsequent sorting. The result of our comparison therefore also demonstrates the need to ensure uniformity in the selection of equipment and quantified recording and processing in future sampling. However, very isolated findings of some taxa could also indicate their restricted distribution and thus might provide evidence of faunistic differences in the meiofaunal communities on various seamounts (including those at the Langseth Ridge) and islands even at major taxon level.

Our comparison of the density values of Nematoda and benthic Copepoda from the deep-sea plains and from various islands and seamounts provided a remarkable trend of increasing densities with increasing depths (Figs. 13 and

14) that, referring to meiofauna, at least partially calls into question the role of seamounts and oceanic islands as productive "oases" (cf. e.g. Rowden et al. 2010a, b; Zeppilli et al. 2014; Tojeira et al. 2025) in the middle of the "desert-like" high and deep sea. The fact that the deep sea is no longer regarded as a hostile, species-poor area of our planet, but instead harbours an extraordinarily high diversity of species, at least in certain taxa (e.g. Ramirez-Llodra et al. 2024), has also been demonstrated for the meiobenthos (e.g. Rose et al. 2005; George et al. 2014). It has also been proven that species diversity correlates very strongly with the spatial density of individuals (Azovsky et al. 2012; George et al. 2014), which in turn—apart from the particle size of the sediment as a remarkable variable (Coull 1988)–is strongly dependent on the nutrient and food supply (e.g. Coull 1988; Giere 2009; Azovsky et al. 2012; George et al. 2014; Zeppilli et al. 2018). This, in turn, is richer near the coast than in high seas regions or in the deep sea (see George et al. 2014 and references therein) and reflected by a decrease of meiobenthic abundance and biomass with increasing depth (Mokievsky et al. 2004; Mokievskii et al. 2007). Against this background, the results of our density comparison were somewhat surprising, although they underpin the findings regarding hadal meiofauna by Zeppilli et al. (2018).

With regard to the area-related abundance of Nematoda and benthic Copepoda, a latitudinal density gradient could not be identified. Although we found the highest peak values at the poles (Fig. 13), the northern and southern regions showed no gradual change in density values, which was not surprising given the present mixture of deep-sea and shallow-water regions (seamounts, island shelves). However, bathymetric sorting (Fig. 14) provided revealing information: The mean density values of Copepoda and Nematoda only correspond to a limited extent with the results of other studies. Density values between about 100 and 200 ind./10 cm^2, as found on the sandy summit of the Senghor seamount, correspond to similar values from the sublittoral of various continental marine regions (cf. Coull 1988). The nematode densities of the abyssal (Fig. 14) are also in the range for corresponding depths in the Atlantic, as summarised by Vincx et al. (1994). However, the area between ~ 200 m and ~ 300 m, which is equivalent to the upper continental slope and in our comparison mainly comprises the plateau of the Great Meteor Seamount and the 300 m depth line of the investigated Azores Islands, is characterised by a pronounced poverty of Nematoda and Copepoda; both taxa combined (and representing the entire meiofauna) do not even reach a density of 200 ind./10 cm^2, which is much less than in comparable near-continental depths with densities that may reach values between 300 and 1000 ind./10 cm^2 (e.g. Thiel 1972; Coull 1988; Vincx et al. 1994 and references therein).

The results summarised in Figs. 13 and 14 indicate that the Great Meteor Seamount, located in the middle of the subtropical Atlantic, is a very oligotrophic habitat and by no means an "oasis" in the surrounding "marine desert", as pointed out already by, e.g. Hempel (1968), Nellen (1973), Heinz et al. (2004) and Piepenburg and Müller (2004). Although the plateau is located at a depth of only about 300 m, it obviously does not form a basis for increased benthic (primary) production (Piepenburg and Müller 2004), which would lead to the so-called "seamount effect", i.e. an enhanced biomass of both plankton and benthos compared to the surrounding area (e.g. Dower and Mackas 1995; Misic et al. 2012; Zhao et al. 2023). A missing "seamount effect" has been confirmed at the Great Meteor Seamount both for phytoplankton (cf. Tojeira et al. 2025 and references therein), for zooplankton in general (Nellen 1973; Martin and Nellen 2004) and for Calanoida specifically (Fischer 2005), for Foraminifera (Heinz et al. 2004) and for fish larvae (Nellen 1973; Clemmesen and Röhrscheidt 2004; Tojeira et al. 2025). At Condor seamount, Zeppilli et al. (2014) showed that the Nematoda exhibit higher density values along its base (~ 1700 m depth) than at the summit (~ 200 m depth). A "seamount effect" with regard to plankton is also missing at Anaximenes Seamount (Denda and Christiansen 2011) as well as at Sedlo and Seine Seamounts (Hirch 2009), and first studies of the meiobenthos at Josephine Bank in the early 1970s also showed extremely low biomass values (Rachor 1975). The density values for Nematoda and Copepoda summarised here are in accordance with this pattern.

The Azores islands of Flores, Terceira and Santa Maria also showed a very low density of Nematoda and benthic Copepoda at a water depth of around 300 m (George et al. 2021; George 2022). We would have expected higher values here, as we had anticipated that, in contrast to the Great Meteor Seamount, the sublittoral of the islands might benefit from a terrestrial influence (nutrient input from land). This is obviously not the case. Extensive analyses of the island data are currently being carried out as part of the BIODIAZ project (George et al. 2021). However, here we speculate that it may be that such a terrestrial influence, if present at all, does not extend to a depth of 300 m, especially as the shelf around the islands often consists of rocky and stony substrates, with sedimentary areas in between, that are colonised by a diverse sessile filter-feeding fauna. Probably most food particles are already being tapped before they reach the seabed at a depth of 300 m, which could help to explain the low density of Copepoda and Nematoda.

In contrast, the Arctic Langseth Ridge with its Northern Mount, Central Mount and Karasik Seamount, which we have investigated, proves to be a productive "hot spot", whose meiofauna density values are many times higher than in other shelf areas and deep-sea plains of the high Arctic

(e.g. Silberberg et al. 2025, see also Mokievskii et al. 2007), and which needs not fear comparison with the tropical Senghor seamount (Kieneke et al. 2025) and which, at least as far as the Nematoda are concerned, clearly surpasses the subtropical Condor seamount (Zeppilli et al. 2014). This may seem surprising at first, because within the area of investigations, north of 85°N, no indication was found of a lateral input of organic material from primary production at the ice-edge and along the continental margins (Soltwedel and Schewe 1997). However, it becomes understandable, if we keep in mind that large parts of this central Arctic ridge are colonised by a megafauna dominated by bacteriosponges of the taxon Tetractinellida, with very high biomass production predominantly based on autotrophic symbionts (Morganti et al. 2022; Stratmann et al. 2022). Furthermore, these highly productive bacteriosponges seem to be part of a "sponge loop", which ends with bacterial mat overgrowth and finally decaying of sponge individuals (Stratmann et al. 2022). Decaying sponge tissue will release a high amount of organic matter, nutrients and even already a microbial community that could serve as a food source for many meiobenthic species inhabiting the STM substratum, not to forget that the spicules and tubes of the associated epizoic polychaetes are the basis of the STM itself. In this sense, the most abundant megafaunal sponge species of the LR, i.e. *Geodia parva*, *G. hentscheli* and *Stelletta rhaphidiophora* (see Morganti et al. 2022), could even be regarded as bioengineers.

The inclusion of density values in a comparison of the meiobenthic seamount communities thus indicates that seamounts as singular entities, which apart from their own shape, size and height are exposed to completely different environmental conditions depending on their location, are by no means characterised by similar meiofaunal communities. We conclude that hypothesis $H_0 3$ must be rejected and extended beyond the Langseth Ridge: seamounts per se do not harbour similar meiofaunal communities.

Conclusion

The position of the studied seamount chain of the Langseth Ridge at the central Arctic Ocean with peculiar climate and hydrographic conditions and a considerable geographic isolation is itself quite unique. Even more, the dense colonisation of the summits with megafaunal bacteriosponges and their associated fauna, and the cover of the seafloor with the dense spicule-tube-mat deriving from debris of this fauna, are making the Karasik Seamount and the neighbouring summits an exceptional deep-sea biotope. Our analyses of the major taxa of the benthic meiofauna demonstrated that despite a clear heterogeneity among the stations— sometimes the fauna of closely neighbouring samples showed a

maximum dissimilarity—there is much likely one meiobenthic community inhabiting the Langseth Ridge. A closer look to the different substrate types, the spicule-tube mat, the soft sediment covered by this mat, and sheer deep-sea sediment, uncovered significant differences on the level of the major meiobenthic taxa. While the absence of certain taxa may be a biassed result due to the analysis of still too few samples, the abundances and the dominances of certain taxa differ considerably between the three substrates. The most obvious effect is visible on the soft sediment underneath the spicule-tube-mat, may be because it is in a way "shielded" from the seafloor surface and the water column. Anyway, we expect even more significant effects on the actual species composition, since the spicule-tube-mat provides a habitat comparable to the interstitial space between sand grains. In such a sense, one could regard the megafaunal sponge community of the Langseth Ridge as bioengineers. Future studies with a deeper taxonomic resolution on the genus and species level are urgently needed to further understand the role of this peculiar biotope.

A qualitative comparison of the meiobenthos communities of 12 seamounts and islands (the three seamounts of the Langseth Ridge combined) shows that just less than 26% of the 27 reported major taxa could be detected everywhere, but around 48% on only half of the elevations. Those of them that were documented only sporadically may actually have a restricted to very restricted distribution. For others, however, which are only missing on individual seamounts or islands, it is reasonable to assume that they have simply not been recorded or have been overlooked. Future studies will have to show whether the existing gaps can be filled.

When comparing our density data of the two dominant taxa, viz. the Nematoda and the Copepoda, from the Langseth Ridge with those of other study sites across the whole Atlantic Basin including the Mediterranean, an interesting pattern was observable. There was a clear response of the densities towards depth, with comparably low but constant values down to the deeper shelf at about 300 m, followed by much higher, but strongly fluctuating values in depth ranges from the continental slope down to bathyal depths. In the abyssal zone, densities were likewise high, but much more constant between different regions. The different supply with nutrients in different depth zones, which also often correlate with the distance to the coast, could be an explanation for this pattern. However, this comparison also showed that the density values of Nematoda and Copepoda differ considerably between different seamounts and island shelfs, i.e. there is no "general seamount meiofauna community" per se.

Declarations

References

Achtziger R, Nigmann U, Zwölfer H (1992) Rarefaction-Methoden und ihre Einsatzmöglichkeiten bei der zooökologischen Zustandsanalyse und Bewertung von Biotopen. Zeitschr Zool Natursch 1:89–105

Araujo TQ, Hochberg R (2021) Marine Gastrotricha of the Azores: updated checklist from São Miguel Island. Açoreana 11:57–77

Azovsky AI, Garlitska LA, Chertoprud ES (2012) Broad-scale patterns in local diversity of marine benthic harpacticoid copepods (*Crustacea*). Mar Ecol Prog Ser 460:63–77. https://doi.org/10.3354/meps09756

Barnett PRO, Watson J, Connelly D (1984) A multiple corer for taking visually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol Acta 7(4):399–408

Bartsch I (2003) Lohmannellinae (*Halacaridae*: *Acari*) from the Great Meteor Seamount (Northeastern Atlantic). Description of new species and reflections on the origin of the seamount fauna. Mitt Hamb Zool Mus Inst 100:101–117

Boetius A, Purser A (2017) The expedition PS101 of the research vessel POLARSTERN to the Arctic Ocean in 2016. Rep Polar Mar Res 706:1–230. https://doi.org/10.2312/BzPM_0706_2017

Boetius A, Roessler S, Tardeck F (2017) The expedition PS101 of the research vessel POLARSTERN to the Arctic Ocean in 2016.

Rep Polar Mar Res 706:36–40. https://doi.org/10.2312/BzPM_0706_2017

Bogorov WG (1927) Zur Methodik der Bearbeitung des Planktons. (Eine neue Kammer zur Bearbeitung des Zooplanktons). Russ Hydrobiol Zh 6:193–198

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27(4):325–349

Büntzow M (2011) Vergleichende gemeinschaftsanalytische und taxonomische Untersuchungen der Harpacticoidenfauna der Seeberge „Sedlo" und „Seine" (nördlicher Mittelatlantik). Doctoral thesis, Carl von Ossietzky-Universität

Cerca J, Purschke G, Struck TH (2018) Marine connectivity dynamics: clarifying cosmopolitan distributions of marine interstitial invertebrates and the meiofauna paradox. Mar Biol 165:1–21. https://doi.org/10.1007/s00227-018-3383-2

Chen GT, Herman RL, Vincx M (1999) Meiofauna communities from the Straits of Magellan and the Beagle Channel. Sci Mar 63(1):123–132

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral J Ecol 18:117–143

Clausen C (2004) Gastrotricha from the Faroe Bank. Sarsia 89:423–458. https://doi.org/10.1080/00364820410002677

Clemmesen C, Röhrscheidt H (2004) Does the Great Meteor Seamount affect growth and condition of fish larvae, with special reference to *Vinciguerria nimbaria*? Arch Fish Mar Res 51(1–3):187–200

Coull BC (1988) Ecology of the marine meiofauna. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington DC, pp 18–38

Denda A, Christiansen B (2011) Zooplankton at a seamount in the eastern Mediterranean: distribution and trophic interactions. J Mar Biol Assoc U K 91(1):33–49. https://doi.org/10.1017/S0025315410001153

Diehl A, Albers E, German CR, Hand KP, Bach W (2017) The expedition PS101 of the research vessel POLARSTERN to the Arctic Ocean in 2016. Rep Polar Mar Res 706:41–50. https://doi.org/10.2312/BzPM_0706_2017

Dower JF, Mackas DL (1995) „seamount effects" in the zooplankton community near Cobb Seamount. Deep-Sea Res I 43(6):837–858

Fischer L (2005) Der Einfluss der Großen Meteorbank auf die Ernährungsbiologie und Verteilung dominanter Calanoida (*Crustacea*, *Copepoda*). Rep Polar Mar Res 499:1–180

Gad G (2004a) The Loricifera fauna of the plateau of the Great Meteor Seamount. Arch Fish Mar Res 51(1–3):9–29

Gad G (2004b) Diversity and assumed origin of the Epsilonematidae (*Nematoda*) of the plateau of the Great Meteor Seamount. Arch Fish Mar Res 51(1–3):30–42. https://doi.org/10.1007/s12526-009-0007-6

Gad G (2009) Colonisation and speciation on seamounts, evidence from Draconematidae (*Nematoda*) of the Great Meteor Seamount. Mar Biodiv 39:57–69. https://doi.org/10.1007/s12526-009-0007-6

Gad G, Schminke HK (2004) How important are seamounts for the dispersal of interstitial meiofauna? Arch Fish Mar Res 51(1–3):43–54

George KH (1999) Community analysis of the harpacticoid fauna of the Magellan Region, as well as first comparisons with Antarctic associations, basing on similarity analyses. Rep Polar Res 327:1–187

George KH (2004) Description of two new species of *Bodinia*, a new genus *incertae sedis* in Argestidae Por, 1986 (*Copepoda*, *Harpacticoida*), with reflections on argestid colonization of the Great Meteor Seamount plateau. Org Divers Evol 4:241–264. https://doi.org/10.1016/j.ode.2004.02.003

George KH (2005) Sublittoral and bathyal Harpacticoida (*Crustacea*: *Copepoda*) of the Magellan region. Composition, distribution and species diversity of selected major taxa. Sci Mar 69(2):147–158

George KH (2013) Faunistic research on metazoan meiofauna from seamounts—a review. Meiofauna Mar 20:1–32

George KH (2022) The meiofauna of the Eratosthenes Seamount (eastern Mediterranean Sea)—first insights into taxa composition, distribution, and diversity. Mar Biodivers 52:62. https://doi.org/10.1007/s12526-022-01295-z

George KH, Schminke HK (2002) Harpacticoida (*Crustacea*, *Copepoda*) of the Great Meteor Seamount, with first conclusions as to the origin of the plateau fauna. Mar Biol 144:887–895. https://doi.org/10.1017/s00227.002.0878.6

George KH, Veit-Köhler G, Martínez Arbizu P, Seifried S, Rose A, Willen E, Bröhldick K, Corgosinho PH, Drewes J, Menzel L, Moura G, Schminke HK (2014) Community structure and species diversity of Harpacticoida (*Crustacea*: *Copepoda*) at two sites in the deep sea of the Angola Basin (Southeast Atlantic). Org Divers Evol 14:57–73. https://doi.org/10.1007/s13127-013-0154-2

George KH, Boetius A, Bäger J, Barz J, Dannheim J, Hentschel U, Kieneke A, Molari M, Nordhausen A, Purser A, Rapp AT, Schmidtmann L, Schramm F, Slaby B, Vonnahme T, Wegener G, Wollenburg J (2017) The expedition PS101 of the research vessel POLARSTERN to the Arctic Ocean in 2016. Rep Polar Mar Res 706:92–120. https://doi.org/10.2312/BzPM_0706_2017

George KH, Pointner K, Packmor J (2018) The benthic Copepoda (*Crustacea*) of Anaximenes Seamount (eastern Mediterranean Sea)—community structure and species distribution. Prog Oceanogr 165:299–316. https://doi.org/10.1016/j.pocean.2018.06.006

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd edition. Springer Verlag, Berlin

Górska B, Grzelak K, Kotwicki L, Hasemann C, Schewe I, Soltwedel T, Włodarska-Kowalczuk M (2014) Bathymetric variations in vertical distribution patterns of meiofauna in the surface sediments of the deep Arctic ocean (HAUSGARTEN, Fram strait). Deep Sea Res i: Oceanogr Res 91:36–49. https://doi.org/10.1016/j.dsr.2014.05.010

Gutzmann E, Martínez Arbizu P, Rose A, Veit-Köhler G (2004) Meiofauna communities along an abyssal depth gradient in the Drake Passage. Deep Sea Res Part II Top Stud Oceanogr 51(14–16):1617–1628. https://doi.org/10.1016/j.dsr2.2004.06.026

Hammer Ø, Harper DAT, Ryan PD (1999–2022) PAST: paleontological statistics software package for education and data analysis. Palaeont Electr 4(1):1–9

Heinz P, Ruepp D, Hemleben C (2004) Benthic foraminifera assemblages at Great Meteor Seamount. Mar Biol 144:985–998. https://doi.org/10.1007/s00227-1257-7

Heip C, Warwick RM, Carr MR, Herman PMJ, Huys R, Smol N, van Holsbeke K (1988) Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord. Mar Ecol Prog Ser 46:171–180

Hempel G (1968) Biologische Arbeiten auf den Atlantischen Kuppenfahrten 1967 von FS "Meteor". Naturwiss Rundsch 3:108–113

Herman RL (1989) Structure of meiofauna communities in the southern bight of the North Sea. Mede Koninklijke Acad Wetensch Lett Kunst België, Wetensch 4:85–119

Herman RL, Dahms H-U (1992) Meiofauna communities along a depth transect off Halley Bay (Weddell Sea - Antarctica). Polar Biol 12:313–320

Higgins RP, Thiel H (eds) (1988) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington DC

Hirch S (2009) Trophic interactions at seamounts. Doctoral thesis, University of Hamburg

Hurlbert SH (1971) The non-concept of species diversity: a critique and alternative parameters. Ecology 52(4):577–586

Kieneke A, Todaro MA (2021) Discovery of two 'chimeric' Gastrotricha and their systematic placement based on an integrative approach. Zool J Linn Soc 192:710–735. https://doi.org/10.1093/zoolinnean/zlaa117

Kieneke A, George KH, Trokhymchuk RR (2025) The meiobenthic community of Senghor Seamount (Cabo Verde, tropical east Atlantic). J VN Karazin Nat Univ Biol 45:14–26. https://doi.org/10.26565/2075-5457-2025-45-2

Koller S, George KH (2011) Description of a new species of *Zosime* Boeck, 1872 (*Copepoda*: *Harpacticoida*: *Zosimeidae*) from the Great Meteor Seamount, representing one of the few eurybathic Harpacticoida among the distinct plateau and deep-sea assemblages. Meiofauna Marina 19:109–126

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

Lubinevsky H, Hyams-Kaphzan O, Almogi-Labin A, Silverman J, Harlavan Y, Crouvi O, Herut B, Kanari M (2017) Deep-sea soft bottom infaunal communities of the Levantine Basin (SE Mediterranean) and their shaping factors. Mar Biol 164:1–12. https://doi.org/10.1007/s00227-016-3061-1

Martin B, Nellen W (2004) Composition and distribution of zooplankton at the Great Meteor Seamount, subtropical Northeast Atlantic. Arch Fish Mar Res 51(1–3):89–100

Martínez A, Di Domenico M, Leasi F, Curini-Galletti M, Todaro MA, Dal Zotto M, Gobert S, Artois T, Norenburg J, Jörger KM, Núñez J, Fontaneto D, Worsaae K (2019) Patterns of diversity and endemism of soft-bodied meiofauna in an oceanic island, Lanzarote, Canary Islands. Mar Biodivers 49:2033–2055. https://doi.org/10.1007/s12526-019-01007-0

Misic C, Bavestrello G, Bo M, Borghini M, Castellano M, Covazzi Harriague A, Massa F, Spotorno F, Povero P (2012) The "'seamount effect'" as revealed by organic matter dynamics around a shallow seamount in the Tyrrhenian Sea (Vercelli Seamount, western Mediterranean). Deep-Sea Res I 67:1–11. https://doi.org/10.1007/s12526-019-01007-0

Mokievskii VO, Udalov AA, Azovsky AI (2007) Quantitative distribution of meiobenthos in deep-water zones of the World Ocean. Oceanol 47(6):797–813. https://doi.org/10.1134/S0001437007060057

Mokievsky VO, Udalov AA, Azovsky AI (2004) On the quantitative distribution of meiobenthos on the shelf of the world Ocean. Oceanol 44(1):99–109

Morganti TM, Slaby BM, de Kluijver A, Busch K, Hentschel U, Middelburg JJ, Grotheer H, Mollenhauer G, Dannheim J, Rapp HT, Purser A, Boetius A (2022) Giant sponge grounds of Central Arctic seamounts are associated with extinct seep life. Nat Commun 13:638. https://doi.org/10.1038/s41467-022-28129-7

Nellen W (1973) Untersuchungen zur Verteilung von Fischlarven und Plankton im Gebiet der Großen Meteorbank. "meteor"-Forsch-Ergebn D 13:47–69

Packmor J, George KH (2018) Littoral harpacticoida (*Crustacea*: *Copepoda*) of Madeira and Porto Santo (Portugal). J Mar Biol Assoc U K 98(1):171–182. https://doi.org/10.1017/S0025315416001168

Packmor J, Riedl T (2016) Records of Normanellidae Lang, 1944 (*Copepoda*, *Harpacticoida*) from Madeira island support the hypothetical role of seamounts and oceanic islands as "stepping stones" in the dispersal of marine meiofauna. Mar Biodiv 46:861–877. https://doi.org/10.1007/s12526-016-0448-7

Packmor J, Müller F, George KH (2015) Oceanic islands and seamounts as staging posts for Copepoda Harpacticoida (*Crustacea*)—shallow-water Paramesochridae Lang, 1944 from the North-East Atlantic Ocean, including the (re-)description of three species and one subspecies from the Madeiran Archipelago. Progr Oceanogr 131:59–81. https://doi.org/10.1016/j.pocean.2014.11.012

Pfannkuche O, Thiel H (1988) 9. Sample processing. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington DC, pp 134–145

Pfeifer D, Bäumer HP, Dekker R, Schleier U (1998) Statistical tools for monitoring benthic communities. Senckenb Marit 29(1/6):63–76

Pielou EC (1966) Shannon's formula as a measure for species diversity: its use and disuse. Am Nat 100:463–465

Piepenburg D, Müller B (2004) Distribution of epibenthic communities on the Great Meteor Seamount (north-east Atlantic) mirrors pelagic processes. Arch Fish Mar Res 51(1–3):55–70

Plum C, George KH (2009) The paramesochrid fauna of the Great Meteor Seamount (Northeast Atlantic) including the description of a new species of *Scottopsyllus* (*Intermedopsyllus*) Kunz (*Copepoda*: *Harpacticoida*: *Paramesochridae*). Mar Biodiv 39:265–289. https://doi.org/10.1007/s12526-009-0022-7

Pointner K (2015) Description of a new species of *Microcanuella* Mielke, 1994 (*Copepoda*: *Polyarthra*: *Canuellidae*) from the Great Meteor Seamount plateau (subtropical NE Atlantic Ocean), with remarks on the geographical distribution of the genus. Zool Anz 259:97–112. https://doi.org/10.1016/j.jcz.2015.03.007

Pointner K (2017) Description of two new species of *Zosime* (*Copepoda*: *Harpacticoida*: *Zosimeidae*), including remarks on its phylogeny and distribution on the Great Meteor Seamount plateau (North-east Atlantic Ocean). J Nat Hist 51(37–38):2283–2330. https://doi.org/10.1080/00222933.2017.1355493

Pointner K (2018) Ther Great Meteor Seamount (Northeast Atlantic): "stepping stone" or "trapping stone"? Quantitative investigation of the distribution, diversity, and origin of the benthic harpacticoid fauna (Crustacea: Copepoda) of the seamount plateau. Doctoral thesis, Carl con Ossietzky-Universität, Oldenburg

Heiner I (2005) Preliminary account of the loriciferan fauna of the Faroe Bank (NE Atlantic). Biofar Proc. pp 213–219

Ptatscheck C, Traunspurger W (2020) The ability to get everywhere: dispersal modes of free-living, aquatic nematodes. Hydrobiologia 847(17):3519–3547. https://doi.org/10.1007/s10750-020-04373-0

Rachor E (1975) Quantitative Untersuchungen über das Meiobenthos der nordatlantischen Tiefsee. "meteor" Forsch-Ergebn D 21:1–10

Ramirez-Llodra E, Meyer HK, Bluhm BA et al (2024) The emerging picture of a diverse deep Arctic Ocean seafloor: from habitats to ecosystems. Elem Sci Anth 12(1):00140. https://doi.org/10.1525/elementa.2023.00140

Richter K (2019) A new genus and four new species of Cylindropsyllidae Sars, 1909 (*Copepoda*: *Harpacticoida*) from the Great Meteor Seamount plateau (North-East Atlantic Ocean), with remarks on the phylogeny and the geographical distribution of the taxon. Mar Biodiv 49:2223–2266. https://doi.org/10.1007/s12526-019-00953-z

Richter K, George KH (2019) Community structure of Harpacticoida and Canuelloida (*Crustacea*, *Copepoda*) on the Great Meteor Seamount (North-east Atlantic Ocean. J Mar Biol Assoc UK 99(6):1325–1342. https://doi.org/10.1017/S0025315419000444

Rose A, Seifried S, Willen E, George KH, Veit-Köhler G, Drewes J, Moura G, Martínez Arbizu P, Schminke HK (2005) A method for comparing within-core alpha diversity values from repeated multicorer samplings, shown for abyssal Harpacticoida (*Crustacea*: *Copepoda*) from the Angola Basin. ODE 5:3–17

Rowden AA, Schlacher TA, Williams A, Clark MR, Stewart R, Althaus F, Bowden DA, Consalvey M, Robinson W, Dowdney J (2010a) A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. Mar Ecol 31(1):95–106

Rowden AA, Dower JF, Schlacher TA, Consalvey M, Clark MR (2010b) Paradigms in seamount ecology: fact, fiction and future. Mar Ecol 31(1):226–241

Schmidt-Rhaesa A (ed) (2020) Guide to the Identification of Marine Meiofauna. Verlag Dr Friedrich Pfeil, München

Schnier J, Hasemann C (2026) Decadal spatial trends in the feeding-type composition of Arctic deep-sea nematodes at LTER-HAUSGARTEN: a dual classification approach. Deep Sea Res II 226:105601. https://doi.org/10.1016/j.dsr2.2026.105601

Shannon CE, Weaver W (1963) The mathematical theory of communication. University of Illinois Press, Illinois

Shimanaga M, Kitazato H, Shirayama Y (2004) Temporal patterns in diversity and species composition of deep-sea benthic copepods in bathyal Sagami Bay, central Japan. Mar Biol 144:1097–1110. https://doi.org/10.1007/s00227-003-1273-7

Silberberg JR, Piepenburg D, Hasemann C (2025) Creepy-crawlies of the Arctic deep sea: metazoan meiobenthic communities across latitudinal and bathymetric gradients in the western Arctic Ocean. Deep Sea Res Part I Oceanogr Res Pap. https://doi.org/10.1016/j.dsr.2025.104513

Soltwedel T, Schewe I (1997) Activity and biomass of the small benthic biota under permanent ice-coverage in the central Arctic Ocean. Pol Biol 19(1):52–62. https://doi.org/10.1007/s003000050215

Somerfield PJ, Warwick RM, Moens T (2005) Meiofauna techniques. In: Eleftheriou A, McIntyre A (eds) Methods for the study of marine benthos, 3rd edn. Blackwell Science ltd, Oxford, pp 229–272

Stratmann T, Simon-Lledó E, Morganti TM, de Kluijver A, Vedenin A, Purser A (2022) Habitat types and megabenthos composition from three sponge-dominated high-Arctic seamounts. Sci Rep 12:20610. https://doi.org/10.1038/s41598-022-25240-z

Tardeck F, Roessler S (2017) The expedition PS101 of the research vessel POLARSTERN to the Arctic Ocean in 2016. Rep Polar Mar Res 706:18–21. https://doi.org/10.2312/BzPM_0706_2017

Hansen JG (2005) The ongoing investigation of the Faroe Bank tardigrade fauna. Biofar Proc. pp 220–223

Thiel H (1972) Die Bedeutung der Meiofauna in küstenfernen benthischen Lebensgemeinschaften verschiedener geographischer Regionen. Verhandlungsber Deutsch Zool Ges 65:37–42

Todaro MA, Hummon WD (2008) An overview and a dichotomous key to genera of the phylum Gastrotricha. Meiofauna Marina 16:3–20

Todaro MA, Cesaretti A, Dal Zotto M (2019) Marine gastrotrichs from Lanzarote, with a description of a phylogenetically relevant species of *Urodasys* (*Gastrotricha*, *Macrodasyida*). Mar Biodiv 49:2109–2123. https://doi.org/10.1007/s12526-017-0747-7

Tojeira I, Souto M, Kaufmann M, Ramos M, Carreiro-Silva M, Fock HO, George KH, Gerkema T, Morato T, Mouriño B, van Haren H, White M, Xavier JR, Rafael T, Martin B, Cabral H, Lino Costa J, Mohn C (2025) From physics to fish: 50 years of research at great meteor seamount. NE Atlantic Mar Biodiv 55:10. https://doi.org/10.1007/s12526-024-01484-y

Trokhymchuk RR, Kieneke A (2024) New records of deep-sea *Gastrotricha* and *Tardigrada* from Iberian and Canary Basins (Northeast Atlantic) with comments on abyssal meiofauna composition and the meiofauna paradox. J Karazin, Biol 43:66–84. https://doi.org/10.26565/2075-5457-2024-43-6

Vincx M, Bett BJ, Dinet A, Ferrero T, Gooday AJ, Lambshead PJD, Pfannkuche O, Soltwedel T, Vanreusel A (1994) Meiobenthos of the deep northeast Atlantic. Adv Mar Biol 30:1–88

White M, Bashmachnikov I, Arístegui J, Martins A (2007) Physical processes and seamount productivity. In: Picher TJ, Morato T, Hart PJB, Clark MR, Haggan N, Santos RS (eds) Seamounts: ecology, fisheries & conservation. Blackwell Publishing, Oxford, pp 65–84

Yamasaki H, Grzelak K, Sørensen MV, Neuhaus B, George KH (2018) *Echinoderes pterus* sp. n. showing a geographically and bathymetrically wide distribution pattern on seamounts and on the deep-sea floor in the Arctic Ocean, Atlantic Ocean, and the

Mediterranean Sea (*Kinorhyncha*, *Cyclorhagida*). ZooKeys 771:15–40. https://doi.org/10.3897/zookeys.771.25534

Yamasaki H, Neuhaus B, George KH (2019) Echinoderid mud dragons (Cyclorhagida: Kinorhyncha) from Senghor Seamount (NE Atlantic Ocean) including general discussion of faunistic characters and distribution patterns of seamount kinorhynchs. Zool Anz 282:64–87. https://doi.org/10.1016/j.jcz.2019.05.018

Yoder M, de Tandindan Ley IW, Mundo-Ocampo Mann J, Blexter M, Poiras L, de Ley P (2006) DESS: a versatile solution for preserving morphology and extractable DNA of nematodes. Nematol 8:367–376. https://doi.org/10.1163/156854106778493448

Zeppilli D, Bongiorni L, Cattaneo A, Danovaro R, Santos RS (2013) Meiofauna assemblages of the Condor Seamount (North-East Atlantic Ocean) and adjacent deep-sea sediments. Deep-Sea Res Pt II Top Stud Oceanogr 98:87–100. https://doi.org/10.1016/j.dsr2.201308.009

Zeppilli D, Bongiorni L, Santos RS, Vanreusel A (2014) Changes in nematode communities in different physiographic sites of the Condor Seamount (north-east Atlantic Ocean) and adjacent sediments. PLoS ONE 9(12):e115601. https://doi.org/10.1371/journal.pone.0115601

Zeppilli D, Leduc D, Fontanier C, Fontaneto D, Fuchs S, Gooday AJ, Goineau A, Ingels J, Ivanenko VN, Kristensen RM, Cardoso Neves R, Sanchez N, Sandulli R, Sarrazin J, Sorensen MV, Tasiemski A, Vanreusel A, Autret M, Bourdonnay L, Claireaux M, Coquillé V, De Wever L, Rachel D, Marchant J, Toomey L, Fernandes D (2018) Characteristics of meiofauna in extreme marine ecosystems: a review. Mar Biodiv 48:35–71. https://doi.org/10.1007/s12526-017-0815-z

Zhao R, Zhao F, Feng L, Fang JK-H, Liu C, Xu K (2023) A deep seamount effect enhanced the vertical connectivity of the planktonic community across 1,000 m above summit. J Geophys Res 128:e2022JC018898. https://doi.org/10.1029/2022JC018898

George KH, Arndt H, Wehrmann A, and Ávila SP, Baptista L, Berning B, Bruhn M, Carvalho F, Creemers M, Defise A, Hermanns K, Hohlfeld M, Iwan F, Janßen T, Jeskulke K, Kagerer M, Kaufmann M, Kieneke A, Loureiro C, Madeira P, Meyer C, Narciso A, Ostmann A, Pieper C, Quartau R, Ramalho R, Richter K, Silva TL, Springer B, Xavier J (2021) Scientific report. BIODIAZ – controls in benthic and pelagic BIODIversity of the AZores. Cruise No. M150. August 27–October 2, 2018. Cádiz (Spain)–Ponta Delgada, São Miguel (Azores). https://www.pangaea.de/expeditions/bybasis/Meteor%20%281986%29