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Benthic communities under methane gradient in the Laptev and East Siberian seas

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Introduction: Methane seeps influence surrounding benthic communities in different ways from slight changes in benthic abundance and biomass to major altering the species composition.

Materials and Methods: We studied benthic communities of 14 methane seep flares in Laptev and East Siberian seas with comparative analysis of species composition and abiotic parameters at the nearby areas not affected by methane seeps. The species diversity was comparable at seep and non-seep sites varying from 3.9 to 39.6 taxa per 100 individuals and from 4.5 to 34.8 taxa per 100 individuals, correspondingly.

Results: The *Laptev Slope* community corresponds with the Polychaeta-community, encircling the upper continental slope area of the entire Siberian Arctic. The *Lower Shelf* community described in this study apparently corresponds with the Ophiocten sericeum community identified in the shelf areas of the Kara, Laptev and East Siberian seas. The *Upper Shelf* community is mostly inhabited by the bivalves species such as *Portlandia arctica, Ennucula tenuis* and *Astarte montagui* communities. The *Estuarine* community, which is the poorest by diversity but has high values of abundance and biomass is directly influenced by the Lena River runoff in terms of lower salinities and higher sedimentation rates.

Discussion: Throughout the study area, the differences between the *Estuarine, Upper Shelf, Lower Shelf* and *Laptev Slope* communities exceeded the differences between the seep and background non-seep areas. Several taxa demonstrated correlations with different environmental factors, including the latitude, depth, temperature, salinity, pH and methane content, not depending on the revealed benthic community. Eight taxa demonstrated correlations with the methane content measured at different sediment depths. Two siboglinids taxa demonstrated high abundances at stations with highest methane content deep in the sediment. At the Siberian shelf, our geochemical data for siboglinid habitats are the first to be published so far.

KEYWORDS

benthic communities, methane seeps, sea shelf, siboglinids, *Oligobrachia*, benthic diversity, Laptev Sea, East Siberian Sea

Introduction

Methane seeps are common in the Arctic Ocean but isolated from each other. Large methane seeps in the East Siberian arctic seas are zones of massive methane bubble emission with dissolved seawater methane concentrations elevated by factors of up to >100 above what would be expected from background (Shakhova et al., 2010). Recent discoveries with sonar images and geochemical quantification allow to suggest that the subsea permafrost is now thawing and releasing methane (Shakhova et al., 2010a; Shakhova et al., 2014; Shakhova et al., 2015; 2019; Leifer et al., 2017). It means that the permafrost "lid" is clearly perforated, and sedimentary CH_4 is escaping to the water column and the atmosphere. The observed range in CH_4 emissions associated with different degrees of subsea permafrost disintegration implies substantial and potent emission enhancement in the East Siberian arctic seas as the process of subsea permafrost thawing progresses with time (Leifer et al., 2017; Shakhova et al., 2017).

In the western part of the Arctic Ocean, methane seeps have been studied in some detail, including local benthic communities (Levin et al., 2000; Gebruk et al., 2003; Dando, 2010). Methane seep communities are different from common deep-sea communities. Benthic diversity at the cold seeps compared to the areas not affected by methane seepage, i.e., the background sites, is very different. Generally, the diversity index is lower within the seep areas (Levin, 2005). However, locally, the increased habitat heterogeneity can increase the overall benthic diversity (Gebruk et al., 2003; Levin, 2005; Sen et al., 2019). In the vicinity of deep-sea methane seeps, there are endemic species and taxonomic groups; in addition to them, the species diversity of common allochthonous invertebrate species increases (Gebruk et al., 2003; Baranov et al., 2020; Vedenin et al., 2020). At shallow depths, the inhabitants of methane seeps do not have obligate and seep-specific features (Dando, 2010; Kokarev et al., 2023).

Several seeps are known in the eastern part of the Arctic Ocean (Shakhova et al., 2010; Lobkovsky et al., 2022), and studies of the composition of benthic communities and endemic species have been conducted on them (Vedenin et al., 2020). However, benthic communities of the Laptev and East Siberian seas have not been sufficiently studied yet (Sirenko, 1998; Petryashev and Novozhilov, 2004; Sirenko et al., 2004; Sirenko and Denisenko, 2010; Kokarev et al., 2017; Vedenin et al., 2018; Kokarev et al., 2021). The previous surveys at the Siberian shelf and slope with no reference to the methane seepages show that diversity gradient was observed ascending from the coastal areas to the shelf edge (Petryashev and Novozhilov, 2004; Vedenin et al., 2018). The coastal shelf community, mostly inhabited by the bivalves species, corresponded to *Portlandia arctica*, *Ennucula tenuis*, and *Astarte montagui* communities, described in several surveys (Petryashev and Novozhilov, 2004; Sirenko and Denisenko, 2010; Kokarev et al., 2017). The community the Laptev Sea shelf previously described as the *Ophiocten sericeum* community, identified in the shelf areas of the Kara, Laptev, and East Siberian seas, revealed by the trawl samples (Zenkevich, 1963; Sirenko, 1998; Petryashev and Novozhilov, 2004; Sirenko and Denisenko, 2010). At the slope of the Laptev Sea, the community was described by Sirenko (1998) as the Polychaeta community, encircling the upper continental slope area of the entire Siberian Arctic. Although the abundance and biomass values were low within this community, the extrapolated species diversity was the highest within the Laptev slope, corresponding to recent data summarized from the central Arctic Ocean, where diversity maximum was observed at ~200 m to 300 m around the shelf edge (Vedenin et al., 2018, 2021b).

The current work examines the communities of previously studied seepages in the Laptev Sea in more detail; for the first time, the seepage area communities of the East Siberian Sea are studied, as well as a large-scale and accurate benthic survey of background shelf stations. All the seeps were discovered in the Eastern-Siberian arctic seas during the International Siberian Shelf Studies (Semiletov and Gustafsson, 2009). The general properties of massive methane release from these seepage areas and their isotopic signatures were described previously (Shakhova et al., 2015; Sapart et al., 2017; Shakhova et al., 2019; Steinbach et al., 2021).

During the selection, other characteristics of ecosystems were also recorded (bottom salinity, sediments type, concentration of organic matter, and methane in bottom water), so we were able to find out which parameters most influence the distribution of benthic communities on the shelf of the Laptev and East Siberian seas. We hypothesized that the depth (i.e., different depth strata) and the presence of active methane seepage are major factors influencing the structure of benthic communities within the study area.

Materials and methods

A total of 23 stations were obtained in the Laptev and East Siberian seas during the 82^{d} cruise of RV "Akademik Mstislav Keldysh" in October 2020 (Figure 1). Field samplings and experiments were approved by the Ministry of Education and Science of the Russian Federation. The following information was supplied relating to field study approvals: DN-09–54/52 of 29.06.2020.

From one to four "Okean" grabs (0.25 m^2) taken at each station, the coordinates were chosen according to the detected locations of the methane seepages revealed by the acoustic flares (14 stations); control stations were taken in the background areas not affected by methane seepage (nine stations) (Eleftheriou and McIntyre, 2005). Station data with coordinates and depth are shown in Table 1.

All samples were washed onboard through the sieves of 0.5-mm mesh size and later fixed with 4% buffered formalin or with 96% ethanol. All organisms were sorted and identified in the laboratory to the lowest possible taxonomical level, counted, and weighed (wet weight and without decalcification). Polychaetes with calcareous (Spirorbidae) and mucous tubes (Chaetopteridae and Siboglinidae) were weighed with tubes. For the individuals fixed with ethanol, the biomass values were corrected according to coefficients introduced by Brotskaya and Zenkevich (1939).

Species abundance and biomass were calculated to square meters. Data on each species abundance is presented in the Supplementary Files. The similarity among the stations was estimated using the quantitative index of Bray–Curtis (square

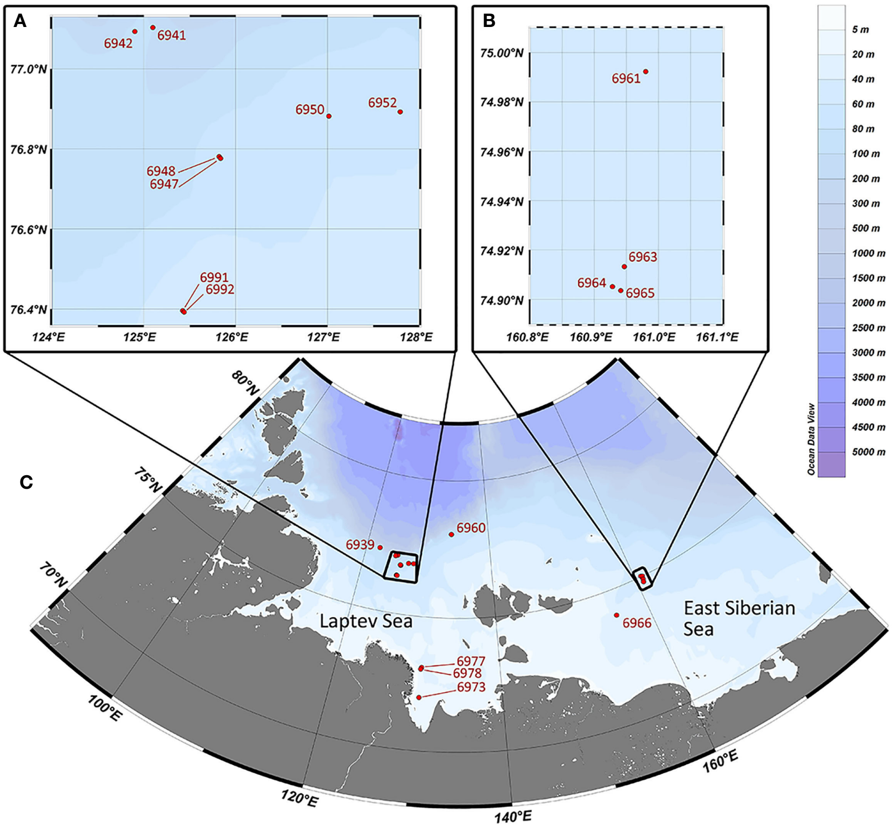

FIGURE 1
Study area and location of sampling stations **(C)**. Enclosed areas show closely located stations at the Laptev Sea shelf **(A)** and the East Siberian Sea shelf **(B)**.

root transformed data, due to high dominance of certain taxa). Dendrogram was built on the basis of similarity matrices (Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method); the cluster analysis was supplemented by non-metric multidimensional scaling (n-MDS). Clusters revealed by these methods were defined as separate benthic communities in terms of quantitative taxonomical similarity. Shade plot was used to visualize the species abundance differences between the stations and species in clusters (McCune et al., 2002; Clarke and Gorley, 2015).

Diversity parameters were estimated by the Simpson index ($1 - \lambda$) (McCune et al., 2002). In addition, due to low abundance and species number in some samples, the extrapolated diversity using Hill numbers ($q = 0$) for 100 individuals was calculated (further referred to as "Hill 100 extrapolated"). Detailed algorithms of extrapolation can be found in the work of Chao et al. (2014). Hill numbers were calculated using original non-transformed number of individuals in each sample. The difference between the benthic communities identified by cluster analysis was verified by the non-parametric Kruskal–Wallis test followed by the Dunn's *post-hoc* test for abundance, biomass, and diversity indices (Lockwood, 1985). The contribution of individual taxa to the Bray–Curtis similarity between the communities was tested using the similarity percentages (SIMPER) analysis. For multiple groups (>2), individual pairwise comparisons were merged with mean dissimilarity and contribution calculated (Clarke and Warwick, 1994).

Environmental measurements were obtained immediately before sampling. Temperature and salinity values were measured in the near-bottom water with the Conductivity-Temperature-Depth (CTD) instrument (SBE 911plus). Methane content and pH values were measured in the sediment at different depths sampled by multicorer instrument. Samples of bottom sediments for determining methane concentrations were taken from the multicorer liner through preliminarily prepared holes with a resolution of 5 cm. The sediment in a volume of 5 cm^3 was placed in hermetically split glass flasks with a volume of 20 mL. Extraction was performed according to the method of static headspace analysis. Thermostating took place at temperatures up to 25°C for at least 30 min. Sample analysis was performed on an SRI-8610c gas chromatograph equipped with a module with Helium Ionization Detector/Thermal Conductivity Detector (HID/TCD) and Flame Ionization Detector (FID) detectors. Methane concentrations were calculated according to the method of Yamamoto et al. (1976) modified by Wiesenburg and Guinasso (1979) using the calculated methane solubility constants. Weight control was additionally carried out for each sediment sample. Under laboratory conditions (20°C), the moisture content and specific gravity required in the calculations were determined.

The determination of pH in bottom sediments is carried out with a portable pH meter (Hanna, HI 991300, UK). Measurements were made according to the manufacturer method. The electrodes

TABLE 1 Station data with date, coordinates, depths, sampled areas, and environmental measurements.

Station	Date (DD/MM/YYYY)	Latitude	Longitude	Depth (m)	Area sampled (m^2)	Seep/ Background	Temperature (°C)	Salinity (psu)	CH_4 at 1–3 cm (µM/L)	CH_4 at 6–9 cm (µM/L)	pH at 1–3 cm	pH at 6–9 cm
6939	06/10/2020	77.2845	122.0958	293.5	0.50	Seep	1.26	30.27	0.06	1.18	–	–
6941	07/10/2020	77.1020	125.0953	364.0	0.25	Seep	2.05	29.47	0.01	0.05	6.83	6.65
6942	07/10/2020	77.0928	124.9023	193.0	0.50	Seep	1.21	30.08	–	–	–	–
6946	08/10/2020	77.1435	126.7982	308.5	0.50	Background	3.38	28.35	0.05	0.94	7.32	7.69
6947	08/10/2020	76.7758	125.8280	72.0	0.50	Seep	3.41	24.38	1334.62	1198.14	7.14	8.16
6948	08/10/2020	76.7778	125.8212	72.5	0.25	Seep	3.58	27.77	25.83	32.85	7.23	8.90
6950	09/10/2020	76.8798	127.0150	69.0	1.00	Background	3.44	28.22	1.31	0.15	7.00	8.25
6952	09/10/2020	76.8915	127.7930	64.0	1.00	Seep	2.25	29.46	0.13	2.91	7.12	7.47
6960	10/10/2020	78.0740	133.5973	206.5	0.50	Background	1.79	28.79	–	–	7.41	7.25
6961	13/10/2020	74.9922	160.9798	45.5	0.50	Seep	0.43	25.44	–	–	7.12	7.82
6963	13/10/2020	74.9130	160.9467	45.5	0.25	Seep	0.29	25.44	0.32	0.16	7.10	8.05
6964	13/10/2020	74.9050	160.9277	45.0	0.25	Seep	0.22	25.25	0.43	1.27	7.17	7.33
6965	14/10/2020	74.9040	160.9408	46.0	0.25	Seep	0.27	25.86	0.34	–	7.08	7.46
6966	14/10/2020	74.0532	155.8052	43.0	0.25	Background	0.64	25.04	0.03	0.02	7.10	8.30
6973	17/10/2020	72.0127	130.3295	17.0	0.25	Background	−0.53	19.93	0.01	0.01	7.27	7.47
6977	18/10/2020	73.1122	130.3562	22.5	0.25	Seep	0.49	20.13	0.02	0.02	7.36	7.58
6978	19/10/2020	73.0927	130.2783	22.0	0.25	Seep	1.17	22.79	0.31	0.20	–	–
6980	20/10/2020	73.9903	130.0677	16.5	0.25	Background	–	–	–	–	–	–
6981	20/10/2020	74.5132	130.0677	34.5	0.50	Background	–	–	–	–	7.21	7.68
6983	20/10/2020	75.0378	130.0743	41.0	0.25	Background	–	–	–	–	7.36	7.58
6985	20/10/2020	76.0873	130.0738	51.5	0.25	Background	–	–	–	–	7.26	7.93
6991	21/10/2020	76.3948	125.4217	52.5	0.25	Seep	1.41	27.29	0.01	0.04	7.25	8.13
6992	21/10/2020	76.3923	125.4280	51.5	0.50	Seep	1.57	27.55	0.04	0.04	7.00	7.75

Absent data are marked with hyphen.

were washed with ionized water before measurements, and the instruments were calibrated every 24 h. The measurement error is pH ±0.02.

All resulting values are shown in Table 1. Spearman ranked correlation was calculated between the environmental values and values of total abundance, biomass, diversity indices, and individual species abundances. The p-values were adjusted by the Bonferroni correction (α = 0.05/$\#_{comparisons}$) to avoid the likelihood of type 1 error. The distance-based redundancy analysis (db-RDA) based on the Bray–Curtis dissimilarity matrix followed by Principal Coordinate Analysis (PCoA) was performed to visualize station distribution along the environmental vectors (Borcard et al., 2011). Taxa significantly correlated with the methane content were plotted as with general additive models (GAMs) (Hastie and Tibshirani, 1990).

Statistics was performed using Microsoft Excel 2010 software and original Python 3.8 scripts using NumPy, Pandas, Scipy, Scikit, Math, Matplotlib, and PyGAM libraries (https://www.python.org/downloads/release/python-380/). Maps were built using Ocean Data View software (Schlitzer, 2020).

Results

Description of samples and benthic communities

A total of 11,591 individuals from 209 taxa were obtained from the samples. Total abundance and biomass varied from 16 ind. m^{-2} and 1.03 g ww m^{-2} [station (st.) 6964] to 1,924 ind. m^{-2} and 188.37 g m^{-2} (st. 6977). The macrotaxa contributing most to the total abundance were the polychaetes (the majority of stations) or mollusks (sts. 6965–6981) (Figure 2A). At some stations, polychaetes were dominant in terms of the biomass (sts. 6939 and 6960); mollusks were dominating at sts. 6966–6981 and 6985; at a few stations, the echinoderms were contributing over 50% (st. 6950) or sipunculids (sts. 6961 and 6983) (Figure 2B).

Cluster analysis revealed four groups of stations (Figure 3). The four clusters that we chose were significantly supported by the PERMANOVA with p-values of <0.01. The clusters were named according to their approximate geographic position as the *Laptev Slope*, the *Lower Shelf*, the *Upper Shelf*, and the *Estuarine* communities. Each community contained the stations from both the methane seepage areas and from the background areas. Multidimensional scaling plot demonstrated similar results; however, the Kruskal stress level was rather low indicating poor ordination results (Figure 4). According to the SIMPER analysis, different taxa dominated each of the revealed communities (Table 2). Full pairwise comparisons are available in the Supplementary Files. Kruskal–Wallis test followed by the pairwise Dunn's *post-hoc* comparison demonstrated no significant difference between the revealed communities in the total abundance and biomass. However, significant difference in the Hill 100 extrapolated diversity index was found (Table 3). Below is a brief description of each benthic community.

The *Laptev Slope* community consisted of five stations, located at the upper slope of the Laptev Sea within the 193-m to 364-m-depth range (Figures 3, 4). Values of the total abundance and biomass were the lowest for this community (mean values of <200 ind. m^{-2} and 11 g ww m^{-2}; see Table 3). However, the extrapolated diversity was the highest (mean values over 25 taxa per 100 individuals; see Figures 5, 6). Main dominants in terms of abundance and biomass were the polychaete *Spiochaetopterus typicus*; other abundant taxa included *Phascolion strombus* sipunculids, *Melinna elisabethae* and *Anobothrus gracilis* polychaetes, siboglinids, and *Pseudosphyrapus serratus* tanaid crustaceans (Table 2, Figure 7).

The *Lower Shelf* community contained seven stations, located in the outer shelf of the Laptev Sea at the depth range of 51 m to 73 m (Figures 3, 4). Values of total abundance and biomass were very high (mean values over 600 ind. m^{-2} and 55 g ww m^{-2}; see Table 3). Diversity was also very high with the mean species number of 42 and Hill 100 extrapolated of 24 (Figures 5, 6). Oweniidae polychaetes were dominant at all the *Lower Shelf* stations. At some of them, siboglinids *Oligobrachia* sp. were extremely dominant (over 700 ind. m^{-2} at st.

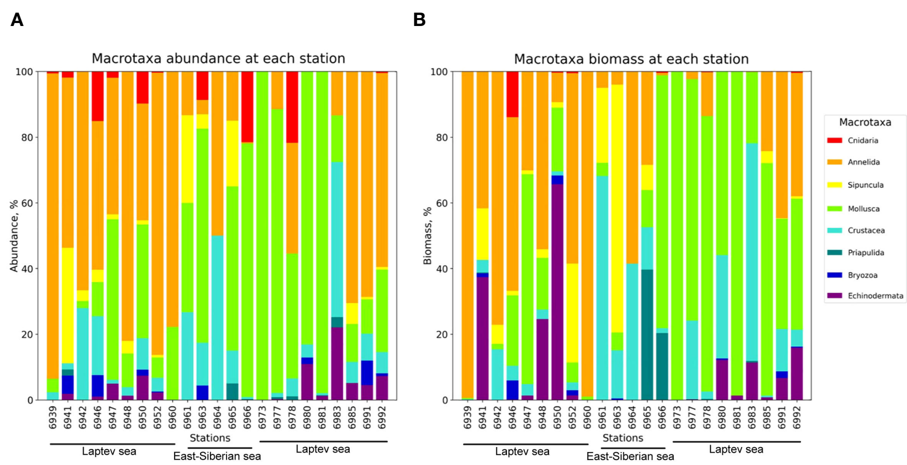

FIGURE 2
Percentage values of macrotaxa at each station. **(A)** Abundance percentage. **(B)** Biomass percentage.

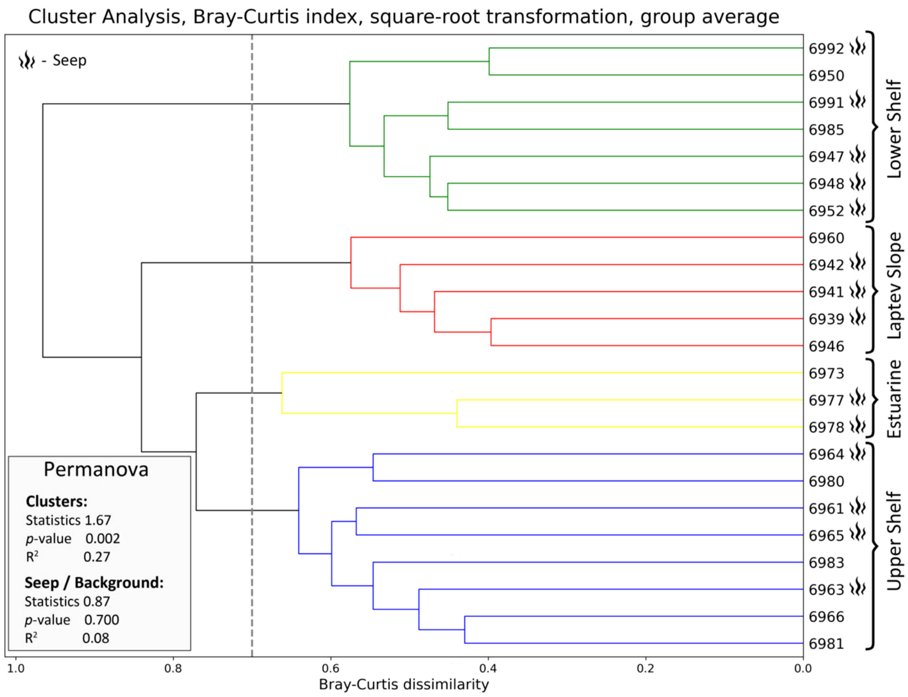

FIGURE 3
Cluster dendrogram of the stations based on the Bray–Curtis similarity index (square root transformed data). Each cluster further referred to as the benthic community is marked with corresponding color; active methane seepage areas are marked with the flame symbol. PERMANOVA results for marked clusters and for active seep/background samples are shown enclosed (sample size, 23; number of permutations, 1,000; number of groups, 4 and 2, correspondingly).

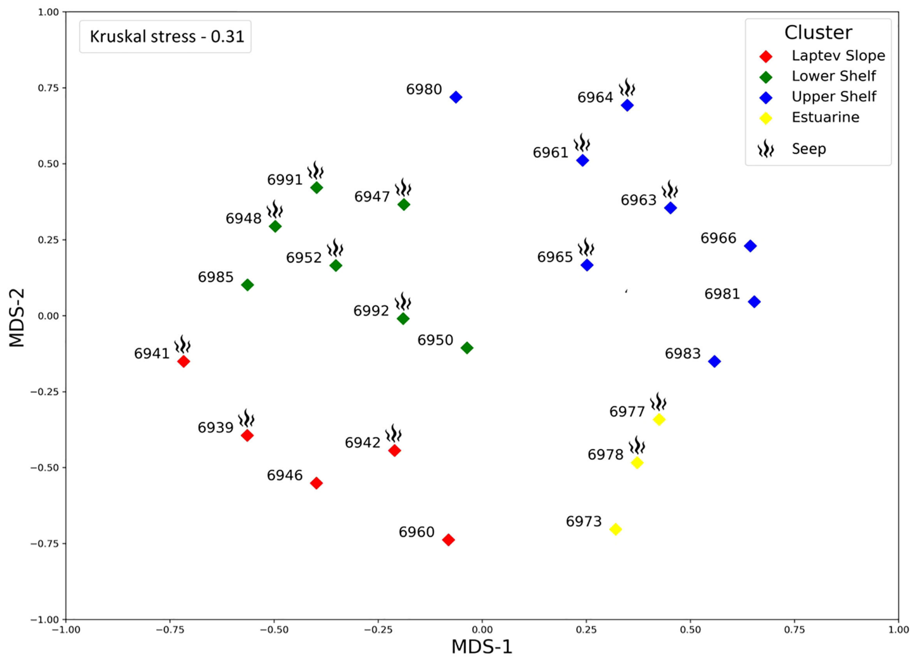

FIGURE 4
Non-metric multidimensional scaling plot of stations, based on the Bray–Curtis similarity index (square root transformed data). Colors and symbols as in Figure 3.

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TABLE 2 Results of the SIMPER analysis with mean values of individual taxon abundance in each of the inferred communities (abundance data).

Species	Mean abundance (ind. m^{-2})				Mean dissimilarity	Standard deviation	Diss./SD ratio	Dissimilarity contribution (%)	Cumulative contribution (%)
	Laptev Slope	*Lower Shelf*	*Upper Shelf*	*Estuarine*					
Portlandia aestuariorum	0	0	0	**605.3**	21.17	12.18	1.73	21.58	21.58
Ennucula tenuis	0	8.0	**161.3**	20.0	6.41	11.61	0.95	6.56	28.14
Oligobrachia sp.	5.6	**133.4**	0	0	6.35	10.05	0.70	6.62	34.76
Myriochele heeri	0.8	**105.4**	0	0	5.60	4.20	1.07	5.84	40.60
Portlandia arctica	0	6.7	**149.5**	0	4.55	8.36	0.56	4.66	45.26
Spiochaetopterus typicus	**52.0**	4.4	0	0	4.34	7.18	0.57	4.44	49.70
Halitholus yoldiaearcticae	0	8.6	**51.0**	26.7	3.60	5.68	0.62	3.69	53.39
Ampharete lindstroemi	1.2	2.9	0	**78.7**	3.36	3.08	0.91	3.43	56.82
Maldane sarsi	0.8	**37.1**	0.5	0	2.71	4.58	0.49	2.83	59.64
Yoldiella lenticula	0.4	**55.0**	0	0	2.61	2.56	0.79	2.72	62.37
Owenia polaris	2.0	**47.9**	0	0	2.48	2.87	0.72	2.59	64.95
Astarte mantagui	0	0.6	**31.5**	0	2.00	5.60	0.36	2.05	67.00
Phascolion strombus	**14.0**	8.6	1.8	0	1.87	3.05	0.68	1.92	68.92
Saduria sabini	0	2.0	**9.8**	5.3	1.33	2.30	0.63	1.35	70.28
Melinna elisabethae	**14.0**	0	0	0	1.28	1.88	0.69	1.31	71.58
Ophiocten sericeum	0	**25.4**	0	0	1.25	0.81	1.54	1.30	72.88
Anobothrus gracilis	**11.2**	0.7	0	0	1.01	1.89	0.49	1.03	73.92
Frigidoalvania sp.	0	**14.3**	0	0	0.89	2.35	0.38	0.93	74.85
Scoletoma fragilis	2.0	**14.3**	0	0	0.84	1.53	0.56	0.88	75.72
Yoldiella solidula	0	**12.9**	0	0	0.75	1.25	0.60	0.79	76.51
Stegophiura nodosa	0	0	**10.0**	0	0.75	1.34	0.56	0.77	77.27
Terebellides sp.	2.4	5.1	0.3	**8.0**	0.72	0.84	0.86	0.74	78.01
Thyasira gouldii	0	5.3	2.0	**17.3**	0.60	0.77	0.75	0.62	78.63
Tharyx sp.	2.8	**5.1**	1.0	2.7	0.57	0.81	0.71	0.59	79.22
Macoma calcarea	0	5.6	1.8	**6.7**	0.57	0.73	0.80	0.59	79.81
Byblis gaimardii	**3.6**	1.6	0	1.3	0.49	0.94	0.63	0.51	80.31

(Continued)

TABLE 2 Continued

Species	Mean abundance (ind. m^{-2})				Mean dissimilarity	Standard deviation	Diss./SD ratio	Dissimilarity contribution (%)	Cumulative contribution (%)
	Laptev Slope	*Lower Shelf*	*Upper Shelf*	*Estuarine*					
Leucon nathorsti	0	1.3	0.5	**6.7**	0.48	0.65	0.70	0.49	80.80
Nephasoma liljeborgii	**4.0**	0	1.0	0	0.46	0.81	0.53	0.47	81.27
Sternaspis scutatus	0	5.4	0	**8.0**	0.46	0.46	1.02	0.47	81.75
Micronephthys minuta	0	**10.0**	0	2.7	0.44	0.89	0.61	0.45	82.20
Nuculana pernula	0	**8.6**	0.3	0	0.43	0.47	0.70	0.45	82.65
Siboglinidae gen. sp.	0	**5.1**	0	0	0.38	0.70	0.55	0.40	83.05
Dacrydium vitreum	**3.6**	0.7	0	0	0.36	0.64	0.55	0.37	83.42
Trochochaeta carica	0	0	0	**5.3**	0.34	0.47	0.73	0.35	83.77
Pseudosphyrapus serratus	**3.6**	0	0	0	0.34	0.60	0.57	0.35	84.12
Chaetozone setosa	**2.8**	1.6	0	1.3	0.33	0.47	0.70	0.34	84.46
Siboglinum hyperboreum	**3.6**	0.3	0	0	0.32	0.38	0.69	0.33	84.79
Cistenides hyperborea	0	**5.1**	0	0	0.32	0.45	0.72	0.33	85.12
Haploops setosa	1.6	**2.0**	0.5	0	0.31	0.65	0.46	0.32	85.44
Aglaophamus malmgreni	0	1.4	**2.0**	0	0.31	0.97	0.44	0.32	85.76
Haploops laevis	0	**5.3**	0	0	0.30	0.29	1.02	0.31	86.07
Eudorella emarginata	0	**5.3**	0.5	0	0.30	0.53	0.52	0.31	86.38
Ampelisca birulai	0	**6.3**	0	0	0.30	0.56	0.53	0.31	86.69
Boreocingula sp.	0	0	**2.0**	1.3	0.28	0.54	0.53	0.29	86.98
Rhizomolgula globularis	0	0	**4.5**	0	0.28	0.79	0.35	0.29	87.27
Harpinia mucronata	**2.8**	0	0	0	0.28	0.65	0.43	0.28	87.55
Caecognathia elongata	**2.8**	0.3	0	0	0.27	0.62	0.49	0.28	87.83
Nephtys ciliata	0	**3.3**	0.8	1.3	0.26	0.43	0.64	0.27	88.09
Ampharete finmarchica	**2.8**	0	0	0	0.25	0.36	0.72	0.26	88.35
Parathyasira dunbari	**2.4**	0.1	0	0	0.24	0.41	0.51	0.25	88.60
Alcyonidium gelatinosum	1.6	**1.7**	0	0	0.24	0.55	0.43	0.25	88.85
Priapulus caudatus	0	0	0.5	**5.3**	0.24	0.29	0.86	0.24	89.09

(Continued)

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TABLE 2 Continued

Species	Mean abundance (ind. m^{-2})				Mean dissimilarity	Standard deviation	Diss./SD ratio	Dissimilarity contribution (%)	Cumulative contribution (%)
	Laptev Slope	*Lower Shelf*	*Upper Shelf*	*Estuarine*					
Scoloplos armiger	0.4	**2.7**	0	1.3	0.23	0.34	0.66	0.23	89.32
Terebellides gracilis	**3.2**	0	0	0	0.23	0.51	0.44	0.23	89.55
Praxillura longissima	**2.4**	0	0	0	0.22	0.36	0.64	0.23	89.78
Philomedes globosus	**2.0**	0.9	0	0	0.22	0.47	0.51	0.22	90.00

Maximum abundance value for each taxon in either of the communities is marked with bold.
Taxa are arranged according to their mean contribution; taxa with cumulative contribution up to 90% are shown.

6952). Among other abundant species, *Maldane sarsi* polychaetes, *Yoldiella lenticula* mollusks, and *Ophiocten sericeum* ophiuroids should be mentioned (Table 2, Figure 7).

The *Upper Shelf* community contained eight stations, being the largest and the most widespread cluster in the sample set. Part of the stations was taken at the Laptev Sea shelf and part of them at the East Siberian Sea shelf; the depth range was 17 m to 46 m (Figures 3, 4). Abundance and biomass values were intermediate for this community (mean: 460 ind. m^{-2}, 48 g ww m^{-2}; Table 3). Diversity values were low (10 species per sample in average, 13 extrapolated taxa per 100 individuals; see Figures 5, 6). Bivalves were dominant by both abundance and biomass, including *Ennucula tenuis*, *Portlandia arctica*, and *Astarte montagui* species. High abundance was also recorded for hydroids *Halitholus yoldiaearcticae* symbiotic with *P. arctica* and for *Stegophiura nodosa* ophiuroids (Table 2, Figure 7).

The *Estuarine* community consisted of only three stations, all located near the Lena River Delta at depths of 17 m to 23 m (Figures 3, 4). This was the poorest community in terms of diversity with high values of abundance and biomass (over 800 ind. m^{-2} and 70 g ww m^{-2}; only 10 species per 100 individuals; see Table 3, Figures 5, 6) due to a few species: bivalves *Portlandia aestuariorum* and polychaetes *Ampharete lindstroemii* (Table 2, Figure 7).

Seep vs. background species composition

Each of the inferred benthic communities consisted of both seep and background stations (Figures 3, 4). The overall community structure was not divided by the presence or absence of the active seepages, the corresponding PERMANOVA analysis showed *p*-values >0.0 5 (Figure 3). Integral community characteristics including the total abundance, biomass, and diversity indices did not differ significantly between the seep and background stations, except for the abundance and biomass within the *Upper Shelf* stations (Table 4). However, additional SIMPER analysis demonstrated certain differences in species composition between the seep and background stations within the *Laptev Slope*, *Lower Shelf*, and *Upper Shelf* communities; the *Estuarine* community consisted of only three stations and was, therefore, too small to run the SIMPER test (Table 5).

In the *Upper Shelf* community, the majority of the taxa showed higher abundance values at the background stations than at the seep stations. In the *Laptev Slope* and *Lower Shelf* communities, most of the species either demonstrated similar abundances at the seep and background station or were less abundant at the seep stations (Table 5). However, several species, including the polychaetes *Spiochaetopterus typicus* and *Anobothrus gracilis*, sipunculid *Phascolion strombus* in the *Laptev Slope* community, and siboglinid *Oligobrachia* sp., polychaete Oweniidae, and gastropod *Frigidalvania* sp., were significantly more abundant at the seep stations (Table 5).

Environmental parameters and benthic communities

The environmental parameters including the temperature, salinity, depth, methane content, and pH were available for not

TABLE 3 Results of the Kruskal–Wallis and Dunn's *post-hoc* tests for total abundance, biomass, and diversity indices in different benthic communities.

Parameters	Mean values				Kruskal–Wallis		Dunn's *post-hoc*
	1 *Laptev Slope*	2 *Lower Shelf*	3 *Upper Shelf*	4 *Estuarine*	H (tie)	*p*	
Total abundance	194	640	457	821	6.05	0.109	–
Total biomass	11.42	55.34	47.93	70.01	6.95	0.073	–
Number of species	24	42	10	13	12.65	0.005	1–3, 2–3, 2–4
Simpson index	0.79	0.81	0.5	0.41	5.94	0.114	–
Hill 100 extrapolated	25.45	23.55	13.38	10.06	8.59	0.035	1–4, 2–4

Mean values are shown for each parameter and each community. Pairs in Dunn's post-hoc column indicate significant comparisons (Dunn's p < 0.05).

all the stations (Table 1). For the distant-based redundancy analysis, we reduced the amount of stations from 23 to 15 in order to include the methane data to the plot (Figure 8). All stations were grouped along two vectors: the Depth (sts. 6939, 6941, and 6946) and more co-directional Salinity + Temperature + CH_4. RDA1 and RDA2 eigenvalues explained 57.8% results, making the ordination acceptable.

Spearman ranked correlation was performed for diversity indices including the Simpson index and Hill 100 extrapolated (Figure 9). According to *p*-values, these parameters were significantly correlated with depth (after the Bonferroni correction) and, to a lesser degree, with temperature and salinity. Total abundance and biomass were not correlated with any of the environmental parameters measured; methane content and pH were also not correlated with any of the community integral parameters (Figure 9).

Over 10 taxa were significantly correlated with either of the environmental factors considered, although only four of them had the significant *p*-values after the Bonferroni correction (Figure 9). Most of them demonstrated positive correlation with temperature and/or depth (three taxa). A few taxa were positively correlated with the methane content: polychaetes *Cistenides hyperborea* and asteroids *Ctenodiscus crispatus* were most correlated with methane concentration at 1-cm to 3-cm sediment depth, and siboglinids *Oligobrachia* sp. and Siboglinidae gen. sp. were most correlated with methane concentration at 6-cm to 9-cm sediment depth (although only Siboglinidae gen. sp. showed significant *p*-values after the Bonferroni correction) (Figure 9).

The abundance of four taxa significantly correlated with the methane content was plotted in relation to methane concentration at different sediment layers; GAMs with Poisson distribution were

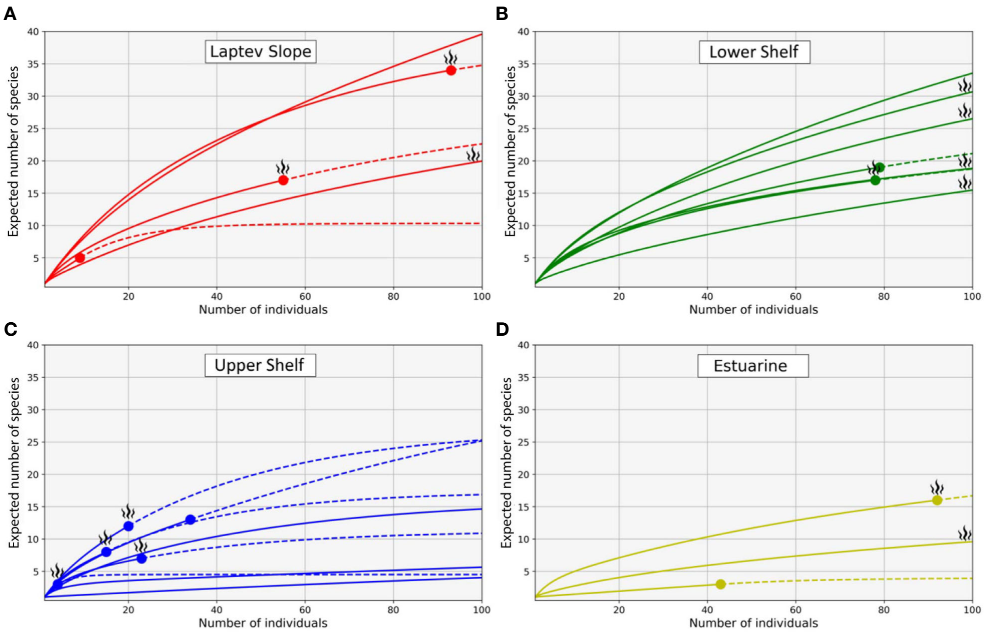

FIGURE 5
Rarefaction curves for the quantitative samples up to 100 individuals with extrapolation based on the Hill numbers (q = 0). **(A)** *Laptev Slope* community; **(B)** *Lower Shelf* community; **(C)** *Upper Shelf* community; **(D)** *Estuarine* community; color corresponds to benthic communities as in Figures 3, 4; active methane seepage areas are marked with flame symbol. Continuous lines indicate true (sample-sized) rarefaction; circles indicate the end of sample; dashed lines indicate the extrapolated rarefaction.

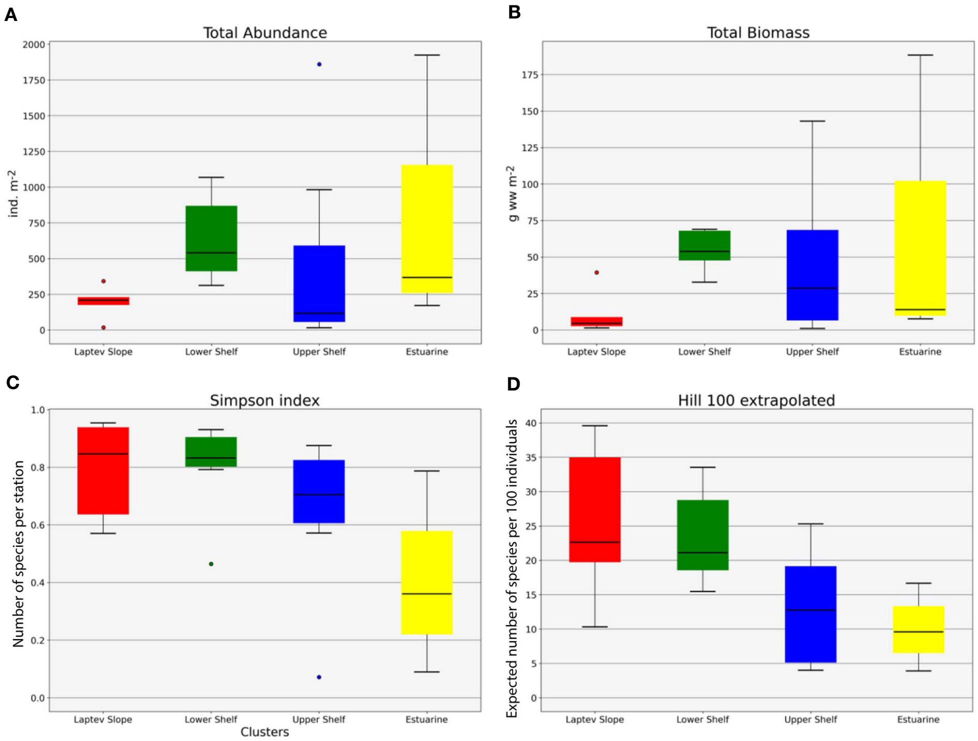

FIGURE 6
Univariative characteristics of identified communities expressed in standard box plots. Values of total abundance **(A)**, biomass **(B)**, Simpson index **(C)**, and Hill 100 extrapolated **(D)** are shown. Each graph contains interquartile ranges (colored boxes), median values (horizontal line inside each box), and minimum and maximum values (lines outside the boxes). Colors are the same as in Figures 3–5.

calculated (Figure 10). For the siboglinids, GAM showed highest values of taxa abundance at methane concentration of ~10^4 to 10^5 μM L^{-1} at sediment depth of 6 cm to 9 cm. For polychaetes, *Cistenides hyperborea* maximum values of abundance, according to GAM, were at ~10^5 μM L^{-1} of methane at sediment depth of 1 cm to 3 cm; for asteroids, *Ctenodiscus crispatus*, the same was observed at methane concentration of ~10 μM L^{-1}. The summary of the GAM models showed significant *p*-values for all the fitted models except for the *C. crispatus* vs. untransformed CH_4 (Table 6).

Discussion

Benthic abundance, biomass, and diversity

Methane seeps are known to influence surrounding benthic communities in various ways from slight changes in benthic abundance and biomass to major altering the species composition (Levin et al., 2000; Dando, 2010). Within the Arctic Ocean, significant increase of the benthic abundance and biomass was reported from several areas of the Atlantic sector of the Arctic, including the Vestnesa Ridge (e.g., five-fold increase in biomass from 0.5 to 3.0 g ww m^{-2} at 1,200 m to 1,500 m; Åström et al., 2018) and cold seeps south off Svalbard (two-fold increase in biomass from ~100 g to ~200 g ww m^{-2} at 200 m to 350 m; Åström et al., 2016). Increased biomass was also reported from the Håkon Mosby mud volcano, although no numbers are currently available (Gebruk et al., 2003). The mentioned cold seeps are located at depths of 200 m to 1,300 m, which is mostly deeper than the samples analyzed in this study. Within the Laptev Shelf, an increase of abundance was previously observed at two geographically compact shallow-water (63 m to 73 m) seep sites named *C15* and *Oden* compared to the background control area (Vedenin et al., 2020). Specifically, a four-fold increase in abundance was observed at the *C15* (from ~2,000 ind. m^{-2} to ~8,000 ind. m^{-2}) and a less significant increase at the *Oden* (from ~2,000 ind. m^{-2} to ~3,000 ind. m^{-2}); biomass changes were statistically insignificant (Vedenin et al., 2020). In this study, sts. 6947 and 6948 were geographically very close to the described *C15* seep site, whereas st. 5952 was close to the *Oden* seep site (Table 1; Vedenin et al., 2020) and demonstrated high values of abundance and biomass (524 ind. m^{-2}, 312 ind. m^{-2}, and 1,018 ind. m^{-2} and 23.9 g ww m^{-2}, 59.0 g ww m^{-2}, and 58.2 g ww m^{-2}, respectively; see the Supplementary Files). However, adding more stations from different areas (both seep and background, including those from the neighboring shelf areas) probably blurred the effect of two previously described sites, likely due to varying activity of the numerous small cold seeps around the *C15* and *Oden*. Overall, across the entire study area from the Lena River Delta to the upper Laptev Sea slope, the differences in abundance and biomass (including those between the seep and background areas) were insignificant (see Table 3, Figures 6A, B).

Benthic diversity at the cold seeps compared to the background is very different. Generally, the diversity expressed in ES-100 or Shannon–Wiener index is lower within the seep areas (Levin, 2005).

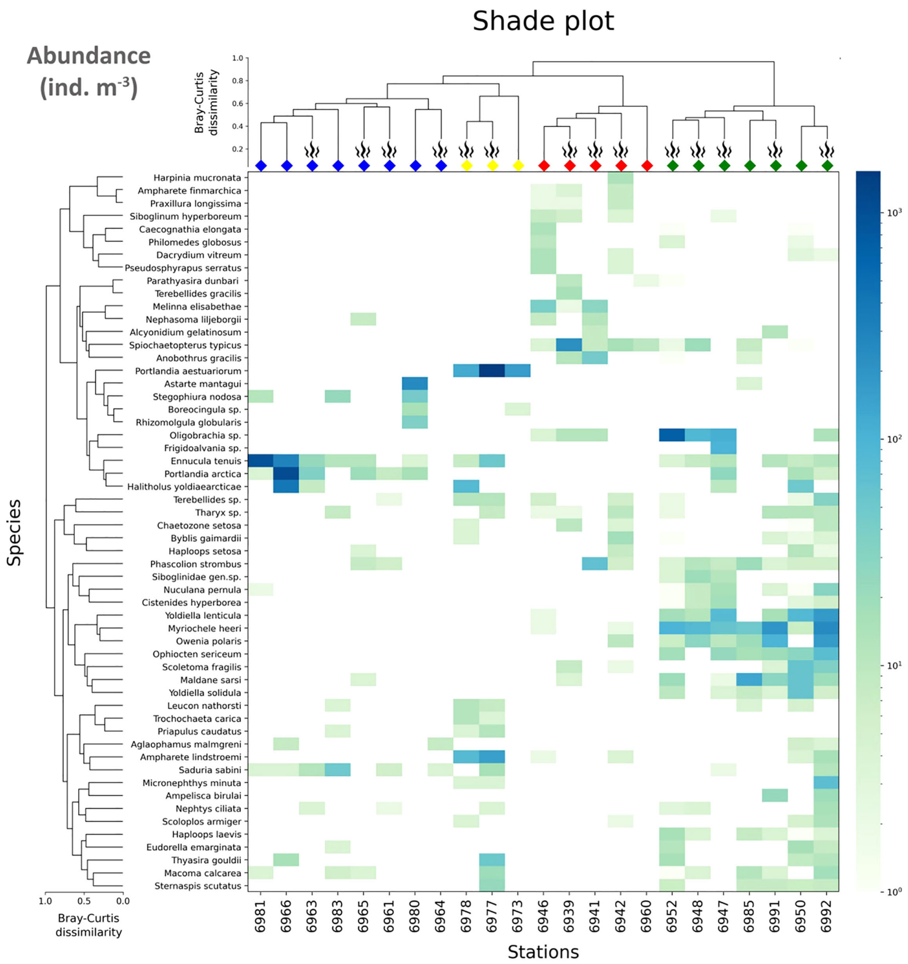

FIGURE 7
Shade plot of species square root transformed abundance at stations. The species list is reduced to 56 taxa presented in the SIMPER table. Order of stations is the same as in Figure 3; symbols and colors for station dendrogram are the same as in Figures 3, 4; taxa are grouped using the UPGMA algorithm based in the index of association. Abundance scale (color bar) is logarithmic.

However, locally, the increased habitat heterogeneity caused, e.g., by the presence of carbonate crusts, can increase the overall benthic diversity (Gebruk et al., 2003; Levin, 2005; Sen et al., 2019). Previously, very high values of the ES-100 and Shannon–Wiener index within the *Oden* seep site were reported with >30 taxa per 100 individuals compared to ~20–25 taxa per 100 individuals in the background (Vedenin et al., 2020). According to our data, this is not correct for the all seep sites used in this study; the species diversity was comparable at seep and non-seep sites varying from 3.9 to 39.6 taxa per 100 individuals and from 4.5 to 34.8 taxa per 100 individuals, correspondingly (Table 3, Figure 5). The diversity was significantly different, however, in different benthic communities, being the lowest near the Lena River Delta and the highest at the Laptev Sea upper continental slope or at the outer shelf, depending on the diversity index used (Table 3, Figure 6). This corresponds with the previous surveys at the Siberian shelf and slope with no reference to the methane seepages, where diversity gradient was observed from the coastal areas to the shelf edge (Petryashev and Novozhilov, 2004; Vedenin et al., 2018).

Benthic communities' characteristics

Four benthic communities revealed in this study (*Laptev Slope*, *Lower Shelf*, *Upper Shelf*, and *Estuarine*) correspond with the previously reported from the Laptev and East Siberian seas during multiple ecological surveys (Sirenko, 1998; Petryashev and Novozhilov, 2004; Sirenko et al., 2004; Sirenko and Denisenko, 2010; Kokarev et al., 2017; Vedenin et al., 2018; Kokarev et al., 2021). Specifically, the *Laptev Slope* community corresponds with the Polychaeta community identified by Sirenko (1998), encircling the upper continental slope area of the entire Siberian Arctic. Sirenko et al. (2004) reported polychaete community dominated by *Spiochaetopterus typicus* with high amount of ophiuroids *Ophiopleura borealis* at the depths of ~200 m to 500 m in the Laptev Sea. In our samples, several polychaete species were dominant at 193 m to 354 m including *S. typicus*, *Anobothrus gracilis*, and *Melinna elisabethae* (Table 2, Figure 7). Although the abundance and biomass values were low within this community, the extrapolated species diversity was the highest within the *Laptev*

TABLE 4 Results of the Kruskal–Wallis and Dunn's for total abundance, biomass, and diversity indices between the seep and background areas.

Cluster	Parameters	Mean values		Kruskal–Wallis		Significance
		Seep	Background	H (tie)	*p*	
All:	Total abundance	542	478	0.02	0.900	-
	Total biomass	51.79	40.85	0.25	0.614	-
	Simpson index	0.39	0.25	0.96	0.328	-
	Hill 100 extrapolated	17.22	19.59	0.57	0.450	-
1 *Laptev Slope*	Total abundance	113	249	1.33	0.248	-
	Total biomass	3.00	17.04	1.33	0.248	-
	Simpson index	0.22	0.21	0.00	1.000	-
	Hill 100 extrapolated	24.95	25.78	0.00	1.000	-
2 *Lower Shelf*	Total abundance	522	688	0.15	0.699	-
	Total biomass	49.23	57.79	0.59	0.439	-
	Simpson index	0.14	0.22	0.04	0.845	-
	Hill 100 extrapolated	25.88	22.62	0.59	0.439	-
3 *Upper Shelf*	Total abundance	859	55	5.33	0.021	+
	Total biomass	86.93	8.93	5.33	0.021	+
	Simpson index	0.47	0.23	2.08	0.149	-
	Hill 100 extrapolated	12.37	14.38	0.33	0.564	-
4 *Estuarine*	Total abundance	172	114	1.50	0.221	-
	Total biomass	13.99	98.03	0.00	1.000	-
	Simpson index	0.97	0.43	1.50	0.221	-
	Hill 100 extrapolated	3.91	13.13	1.50	0.221	-

Slope, corresponding together to the common community ecology paradigm (Weiher and Keddy, 1999; Piraino et al., 1999) and to recent data summarized from the central Arctic Ocean, where diversity maximum was observed at ~200 m to 300 m around the shelf edge (Vedenin et al., 2018, 2021b). This community is influenced (and probably conditioned) by the warm Atlantic waters, enriched with organic carbon and flowing eastward at these depths (Wassmann et al., 2019; Bluhm et al., 2020).

The *Lower Shelf* community described in this study apparently corresponds with the *Ophiocten sericeum* community, identified in the shelf areas of the Kara, Laptev, and East Siberian seas, revealed by the trawl samples (Zenkevich, 1963; Sirenko, 1998; Petryashev and Novozhilov, 2004; Sirenko and Denisenko, 2010). Grab samples, containing fewer members of megafauna, demonstrated the dominance of the bivalves, including *Yoldiella solidula* and *Yoldiella lenticula* and, sometimes, polychaetes Maldanidae (Kokarev et al., 2017; Vedenin et al., 2018). In our samples, species composition was similar, although shifted significantly to the polychaete dominance at seep stations, mostly Oweniidae and Siboglinidae (Table 5).

The *Upper Shelf* community, mostly inhabited by the bivalves species, corresponded to *Portlandia arctica*, *Ennucula tenuis*, and *Astarte montagui* communities, described in several surveys (Petryashev and Novozhilov, 2004; Sirenko and Denisenko, 2010; Kokarev et al., 2017). So far, no direct comparison between the Laptev and East Siberian shelves was published. In our samples, community composition at three stations from the Laptev Sea and at five stations from the East Siberian Sea was surprisingly similar, intermixed at the cluster dendrogram (Figure 3). Located at depths of 17 m to 46 m within the inner Siberian shelf, this community is influenced by the freshwater runoff (Kokarev et al., 2017; Kokarev et al., 2021).

The *Estuarine* community, the poorest by diversity but with high values of abundance and biomass, is directly influenced by the Lena River runoff in terms of lower salinity and higher sedimentation rate values (Drits et al., 2021). Dominated by bivalves, *Portlandia aestuariorum*, this community corresponds to estuarine communities, formed near large Siberian rivers, including Ob, Yenisei, Lena, Kolyma, Khatanga, Mackenzie, and other rivers (Jørgensen et al., 1999; Deubel et al., 2003; Aitken et al., 2008; Sirenko and Denisenko, 2010; Vedenin et al., 2015).

Seep vs. background

Throughout the study area, the differences between the *Estuarine*, *Upper Shelf*, *Lower Shelf*, and *Laptev Slope* communities exceeded the differences between the seep and

TABLE 5 Results of the SIMPER analysis between the seep and background stations within the *Laptev Slope*, *Lower Shelf*, and *Upper Shelf* benthic communities (abundance data).

Species	Mean abundance (ind. m^{-2})		Dissimilarity	Standard deviation	Diss./ SD ratio	Diss. contribution (%)	Cumulative contribution (%)
	Seep	Background					
Laptev Slope							
Spiochaetopterus typicus	**82**	7	17.66	25.16	0.70	20.22	20.22
Phascolion strombus	**23**	0	7.69	10.94	0.70	8.81	29.03
Anobothrus gracilis	**19**	0	5.70	7.30	0.78	6.52	35.55
Melinna elisabethae	10	**20**	5.33	4.97	1.07	6.11	41.65
Byblis gaimardii	**6**	0	2.22	3.70	0.60	2.55	44.20
Oligobrachia sp.	**8**	2	2.11	1.80	1.17	2.42	46.62
Harpinia mucronata	**5**	0	1.73	2.88	0.60	1.98	48.60
Dacrydium vitreum	1	**7**	1.71	1.38	1.23	1.95	50.55
Pseudosphyrapus serratus	1	**7**	1.71	1.38	1.23	1.95	52.51
Nephasoma liljeborgii	4	4	1.57	1.88	0.84	1.80	54.31
Lower Shelf							
Oligobrachia sp.	**187**	0	14.99	19.40	0.77	19.63	19.63
Myriochele heeri	**137**	28	9.04	5.75	1.57	11.84	31.48
Maldane sarsi	14	**95**	8.34	6.19	1.35	10.93	42.40
Yoldiella lenticula	**60**	42	5.00	3.70	1.35	6.55	48.95
Owenia polaris	**63**	10	4.55	4.20	1.08	5.96	54.92
Scoletoma fragilis	8	**30**	2.57	2.65	0.97	3.37	58.29
Yoldiella solidula	5	**33**	2.53	2.41	1.05	3.31	61.60
Halitholus yoldiaearcticae	2	**25**	2.14	2.19	0.98	2.80	64.39
Frigidoalvania sp.	**20**	0	2.13	4.53	0.47	2.79	67.18
Ophiocten sericeum	**27**	22	1.51	1.29	1.17	1.98	69.16
Upper Shelf							
Ennucula tenuis	9	**314**	28.11	37.63	0.75	29.96	29.96
Portlandia arctica	16	**283**	17.21	24.26	0.71	18.34	48.30
Astarte mantagui	0	**63**	12.82	23.00	0.56	13.66	61.96
Saduria sabini	6	**14**	6.48	10.98	0.59	6.90	68.86
Stegophiura nodosa	0	**20**	5.94	5.96	1.00	6.33	75.19
Halitholus yoldiaearcticae	2	**100**	5.57	9.13	0.61	5.93	81.13
Rhizomolgula globularis	0	**9**	1.83	3.29	0.56	1.95	83.08
Tharyx sp.	0	**2**	1.14	2.08	0.55	1.21	84.29
Macoma calcarea	1	**3**	0.87	1.41	0.62	0.92	85.22
Admete viridula	0	**4**	0.81	1.46	0.56	0.87	86.08

Maximum abundance value for each taxon in either of the communities is marked with bold.
First 10 taxa of the SIMPER list are shown for each of the communities.

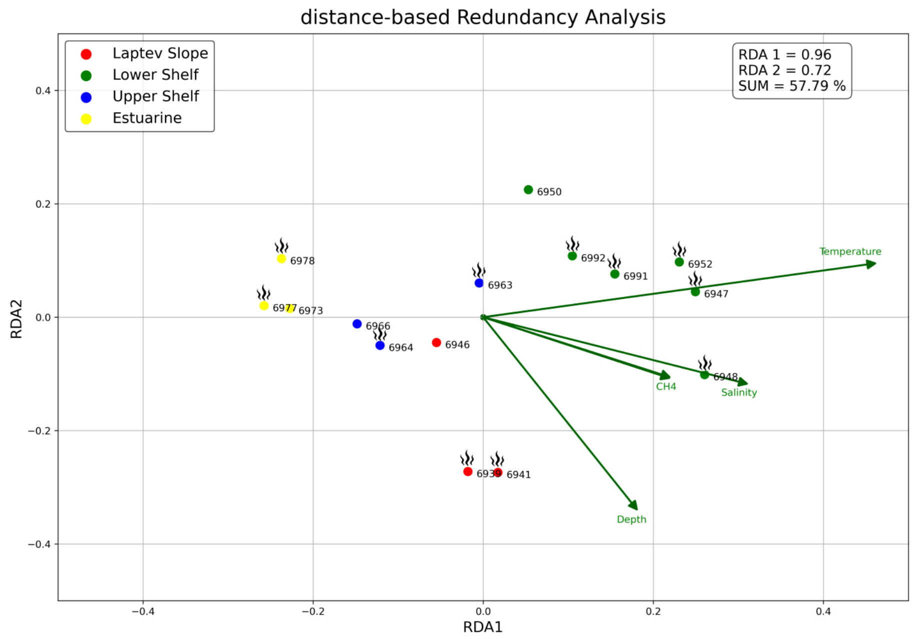

FIGURE 8
db-RDA plot of stations along the depth, temperature, salinity, and methane content (green vectors). Active methane seepage areas are marked with flame symbol. Colors of stations the same as in Figures 3, 4, 7. Response data are calculated by PCoA based on the square-root Bray–Curtis dissimilarity; scaling, 1.

background areas. Total abundance, biomass, and diversity showed no significant differences between the seep and non-seep samples (Table 4). However, within each of the benthic communities (except for the *Estuarine*), certain differences in taxonomical composition were revealed (Table 5). The *Estuarine* community consisted of only three stations, therefore making statistically insignificant SIMPER results (Table 4).

The *Laptev Slope* stations were located at the depth range, where significant peculiarities in species composition are known from the cold seeps worldwide (>200 m; Levin, 2005; Dando, 2010). In the Arctic cold seeps, high abundances of chemosymbiotrophic taxa were reported (mainly different species of Siboglinidae, all obligatory symbiotrophic) from depths exceeding 200 m as it was in the Barents Sea cold seeps (Åström et al., 2016), Vestnesa Ridge (Åström et al., 2018; Sen et al., 2020), Håkon Mosby mud volcano (Gebruk et al., 2003), mud volcanoes of the Beaufort Sea (Paull et al., 2015), and Lofoten-Vesterålen canyons (Sen et al., 2019). Apart from siboglinids, several species of molluscs are known to inhabit cold seeps, including probably symbiotrophic recently extinct Thyasiridae bivalves (west off Svalbard; Åström et al., 2018) and Rissoidae gastropods, grazing at bacterial colonies [at Håkon Mosby mud volcano (Gebruk et al., 2003) and in Lofoten-Vesterålen canyons (Sen et al., 2019)]. Another taxon, sometimes associated with the Arctic cold seeps, is Tanaidacea crustaceans. For the Arctic Ocean, several species were described from the Håkon Mosby mud volcano (Błażewicz-Paszkowycz and Bamber, 2011), although it is not known whether they are restricted to the cold seeps environment. In our samples, only a low amount of *Oligobrachia* sp. and *Siboglinum hyperboreum* siboglinids was found in the seep samples from 193-m to 364-m-depth range (Table 2; Supplementary 1), whereas most of the taxa demonstrated similar densities within outside the active methane seepages. In addition, comparing to the background stations, an incredibly high amount of *Spiochaetopterus typicus* polychaetes was observed at the seep stations (Table 5). Nothing is known about *S. typicus* ability to symbiotrophy; however, certain members of Chaetopteridae family are known to inhabit reduced habitats, e.g., deep-sea hydrothermal vents or whale falls (Nishi and Rouse, 2007; Kiel and Dando, 2009; Nishi and Rouse, 2014). Anyway, *S. typicus* is an extremely widespread species, inhabiting vast areas of the Arctic Ocean shelf and slope (Vedenin et al., 2021a).

The *Lower Shelf* stations were located shallower than the usual faunal response to the methane seepage that occurs. Previously, large quantities of *Oligobrachia* sp. siboglinids were reported from the *C15* and *Oden* seep sites as the shallowest known localities for this species (Baranov et al., 2020; Vedenin et al., 2020). Furthermore, shallow-water localities of different siboglinids were recently discovered in the Kara Sea (Smirnov et al., 2020; Karaseva et al., 2021a) and in the East Siberian Sea (Karaseva et al., 2021b). In our samples (all taken in the Laptev Sea shelf at 51 m to 73 m), significantly higher densities of *Oligobrachia* sp. siboglinids, Oweniidae polychaetes, and *Frigidalvania* sp. gastropods were found at seep stations compared to the background ones, which is in accordance with previously published species lists for the *C15* and *Oden* seep sites (Vedenin et al., 2020). As noted previously, the overall difference between the seep and non-seep *Lower Shelf* samples in this study was less significant than described for the *C15* and *Oden* (see first subsection of the Discussion). A possible explanation is due to larger area covered by stations in this study, therefore, sampling more cold seeps and more background samples.

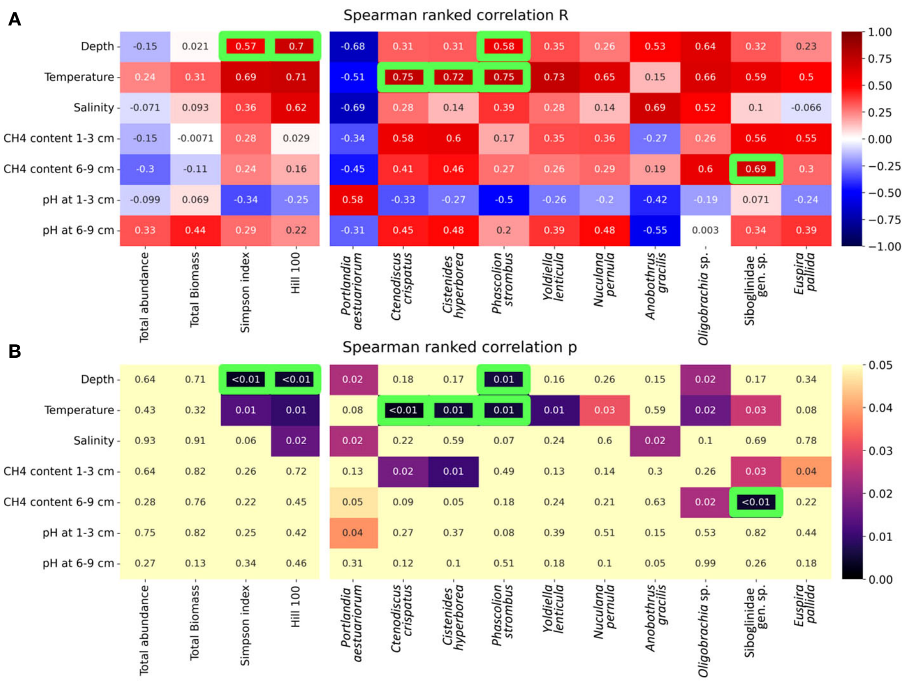

FIGURE 9
Heat maps of Spearman ranked correlation values between the environmental parameters and integral community parameters (total abundance, biomass, and diversity indices) and individual taxon abundances. **(A)** R-values; **(B)** *p*-values. Ten taxa with lowest mean p-values are shown. Green boxes mark the correlations that remained significant after the Bonferroni correction.

Compared to *C15* and *Oden*, other seep sites could be smaller in area or lower in activity, although this is yet to be investigated in future.

The *Upper Shelf* stations (both seep and background ones) were located even shallower and closer to the coast than the *Lower Shelf* stations. In this community, the seep samples demonstrated significantly lower abundance of most of species, compared to the background samples (Table 5). This corresponds with the known distribution patterns of macrobenthos at the shallow coastal cold seeps, like the described for the North Sea pockmarks (Dando et al., 1991), with little or no faunal response to methane presence, or the Baltic Sea pockmarks (Pimenov et al., 2008; Ezhova et al., 2012), where significant depletion of fauna was observed. Many authors agree that the chemosynthesis-derived organic (e.g., from cold seeps or hydrothermal vents) is a major source for benthic consumers only at depths, where the photosynthesis-derived organic is depleted (Powell et al., 1986; Levin, 2005; Tarasov et al., 2005; Dando, 2010). At the shallow-water areas, the chemosynthesis-derived organic input to the macrofauna is usually low or absent, probably due to unfavorable environment (methane or sulfides, toxic for many benthic organisms), as confirmed for the North Sea pockmarks and for Northern California (Dando et al., 1991; Levin et al., 2000); in both areas, the signatures of the chemosynthetic contribution to the macrofaunal diet were little or even absent.

Several taxa demonstrated correlations with different environmental factors, including the latitude, depth, temperature, salinity, pH, and methane content (Figure 9), not depending on the revealed benthic community. The methane content was higher at the seep stations (see Table 1), although the seep/non-seep stations were determined by the acoustic flares, not by the sediment chemical parameters. Eight taxa demonstrated correlations with the methane content measured at different sediment depths with Spearman p-values of <0.03 observed for four species: siboglinids *Oligobrachia* sp., Siboglinidae gen. sp., polychaetes *Cistenides hyperborea*, and asteroids *Ctenodiscus crispatus*. Two latter taxa, although not caught by SIMPER analysis, showed higher abundance within the stations with high methane content near the sediment surface (Figures 10C, D). Based on Figure 10, highest densities of *C. hyperborea* corresponded to methane concentration of ~10^5 µM L^{-1}. C. *crispatus* reached largest quantities at much lower methane concentration of ~10 µM L^{-1}. Both taxa could possibly act as grazers at the seep sites, consuming sediment with chemoautotrophic organic matter. For polychaetes, such behavior was reported for many species in various cold seeps and hydrothermal vents (Sibuet et al., 1988; Levin, 2005). For echinoderms, higher quantities of juvenile specimens were observed within or near the seep sites, e.g., ophiuroids on the continental slope of Chile (Quiroga and Sellanes, 2009). Similar aggregations were reported for holothurians, echinoids, and asteroids of Oregon, California, and Gulf of Mexico (MacDonald et al., 2004; Levin, 2005). The phenomenon of increased abundance of certain widespread taxa around the cold seeps was described by many authors (summarized by Levin, 2005; Dando, 2010).

In contrast to polychaetes and ophiuroids described, two siboglinids taxa (*Oligobrachia* sp. and Siboglinidae gen. sp.) demonstrated high abundances at stations with highest methane content deep in the sediment, measured at 6 cm to 9 cm from the surface (Figures 10A, B). The number of data point for the

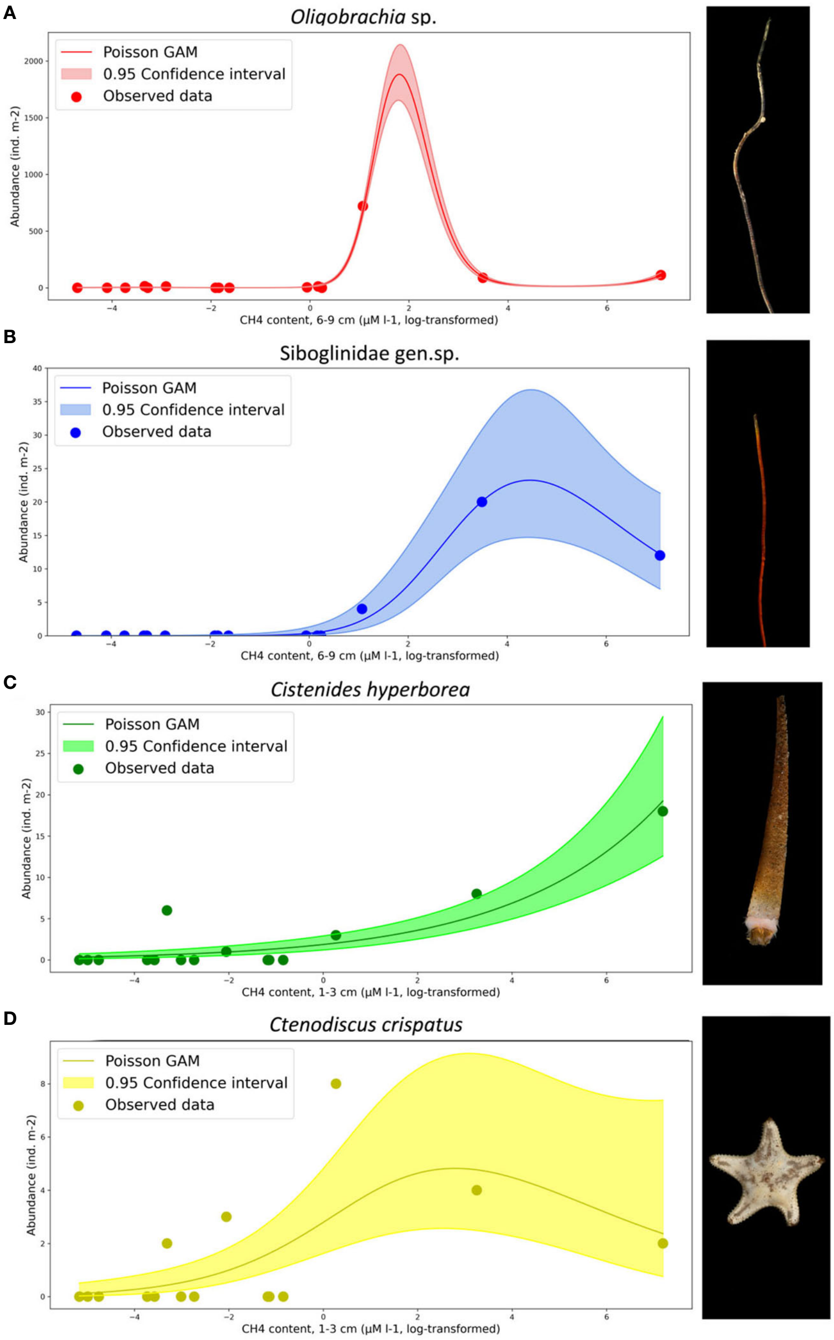

FIGURE 10
Abundance of four taxa in relation to methane concentration (log-log transformed data) with Poisson GAM (general additive model) and confidence GAM interval added. **(A)** *Oligobrachia* sp.; **(B)** Siboglinidae gen. sp.; **(C)** *Cistenides hyperborea*; **(D)** *Ctenodiscus crispatus*. Photos by A. Vedenin.

siboglinids is also small, but both species reached maximum densities at methane concentration of ~10^4 to 10^5 µM L^{-1}. A few correlations between Siboglinidae species have been published so far. For the Antarctic cold seeps in Bransfield Strait, *Sclerolinum* genus was found at methane concentrations of <25 µM L^{-1} (Sahling et al., 2005). In the Skagerrak, siboglinid *Siboglinum poseidoni* reached high densities within the methane concentrations of 300 µM L^{-1} to 3,300 µM L^{-1} (Dando et al., 1994). In the Sea of Okhotsk, *Siboglinum caulleryi* and *Oligobrachia dogieli* siboglinids were found at extremely high concentrations of 4 × 10^6 µM L^{-1} (Karaseva et al., 2020). In the Arctic Ocean, high densities of *Sclerolinum contortum* and *Oligobrachia haakonmosbiensis* siboglinids were found at methane concentration of >2.103 µM L^{-1} (Pimenov et al., 1999; Lein et al., 2000; Smirnov, 2000). At the Vestnesa Ridge, over 2,000 ind. m^{-2} of unidentified siboglinids (belonging to *Oligobrachia* genus; see Sen et al., 2020) were found within the methane concentration of ~10^4 µM L^{-1} measured at 5 cm to 15 cm below the seafloor surface (Åström et al., 2018). At the Siberian shelf, our geochemical data for siboglinid habitats are the first to be published so far.

TABLE 6 Summary of generalized additive models for four species vs. CH_4 sediment content.

Variables			Approximate R^2	Chi. Sq.	*p*-value
Oligobrachia sp.	CH_4 content (6–9 cm)	Untransformed	0.07	40.42	2.05E-10
	CH_4 content (6–9 cm)	Log-transformed	0.05	743.70	< 2E-16
Siboglinidae gen. sp.	CH_4 content (6–9 cm)	Untransformed	0.16	32.90	9.73E-09
	CH_4 content (6–9 cm)	Log-transformed	0.29	68.83	< 2E-16
Cistenides hyperborea	CH_4 content (1–3 cm)	Untransformed	0.73	63.36	1.72E-15
	CH_4 content (1–3 cm)	Log-transformed	0.86	65.52	5.75E-16
Ctenodiscus crispatus	CH_4 content (1–3 cm)	Untransformed	0.07	0.52	0.4710
	CH_4 content (1–3 cm)	Log-transformed	0.01	11.09	8.69E-04

Although an increase in benthic diversity in the cold seep areas has previously been described, this was not confirmed in our studies. This may to be significant for deep seeps communities, which have few sources of organic matter. In addition, this result may be explained by the fact that a larger number of samples in our studies "blurred" the effect of increasing diversity in the area of seeps.

The diversity gradient of benthic communities rather confirmed the previously described patterns of increasing the number of species from coast to continental slope. However, several species, including the polychaetes *Spiochaetopterus typicus* and *Anobothrus gracilis*, sipunculid *Phascolion strombus* in the *Laptev Slope* community, siboglinid *Oligobrachia* sp., polychaete Oweniidae, and gastropod *Frigidalvania* sp., were significantly more abundant at the seep stations.

Further research is planned for studying the trophic features and possible symbiotrophy of individual species together with the microbiome of benthic invertebrates, as well as studying the biodiversity of benthic communities in the East Siberian Sea.

Author's Note

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Field samplings and experiments were approved by the Ministry of Education and Science of the Russian Federation.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

OK: Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – original draft, Writing – review & editing. NR-K: Investigation, Writing – original draft, Writing – review & editing, Conceptualization, Funding acquisition, Methodology. PK: Investigation, Writing – original draft, Writing – review & editing, Data curation, Validation. AO: Data curation, Investigation, Writing – original draft, Writing – review & editing, Formal analysis, Funding acquisition. MF: Formal analysis, Investigation, Writing – original draft, Writing – review & editing. IM: Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. DP: Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. DK: Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. IS: Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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