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Distribution of *Nereilinum murmanicum* (Annelida, Siboglinidae) in the Barents Sea in the Context of Its Oil and Gas Potential

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Abstract: Frenulate siboglinids are a characteristic component of communities living in various reducing environments, including sites with hydrocarbon seeps. High concentrations of hydrocarbons in the sediments of the Arctic basin seas, including the Barents Sea, suggest the presence of a rich siboglinid fauna there. This reflects the fact that microbiological oxidation of methane occurs under reducing conditions, generating high concentrations of hydrogen sulfide in the sediment. This hydrogen sulfide acts as an energy source for the sulfide-oxidizing symbionts of siboglinids. Here we report on the findings of the frenulate siboglinid species *Nereilinum murmanicum* made between 1993 and 2020 in the Barents Sea. These data significantly expand the range of this species and yield new information on its habitat distribution. The depth range of *N. murmanicum* was 75–375 m. The species was most abundant from 200 to 350 m and was associated with temperatures below 3 °C and salinities from 34.42 to 35.07. Most of the findings (43 locations or 74%) fall on areas highly promising for oil and gas production. Twenty-eight locations (48%) are associated with areas of known oil deposits, 22 locations (37%) with explored areas of gas hydrate deposits. *N. murmanicum* was also found near the largest gas fields in the Barents Sea, namely Shtokman, Ludlovskoye and Ledovoye.

Keywords: Siboglinidae; Barents Sea; reducing environment; oil and gas fields

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1. Introduction

The Siboglinidae are a family of sedentary marine annelids whose representatives all lack a digestive tract. Symbiotic bacteria inhabiting a special parenchymal organ—the trophosome—assume the digestive functions [1–3]. Modern taxonomy distinguishes four siboglinid groups: Vestimentifera, Monilifera (genus *Sclerolinum* Southward, 1961), Frenulata, and Osedacinae (genus *Osedax* Rouse, Goffredi & Vrijenhoek, 2004) [4–8]. Representatives of the Osedacinae live on the sunken skeletons of whales and other large vertebrates and have heterotrophic symbionts [9–11]. The trophosome in representatives of Vestimentifera, Monilifera and Frenulata is populated by chemoautotrophic bacteria. The possible presence of both sulfide and methane-oxidizing bacteria has currently been shown for representatives of the latter two groups [12–16].

Representatives of Vestimentifera inhabit hydrothermal oases and cold hydrocarbon seeps. The presence of sulfide-oxidizing symbionts was initially shown for vestimentiferans [17,18]. More recent data indicate that the endosymbionts of at least some vestimentiferans are capable of switching between autotrophic and heterotrophic metabolism, or might be mixotrophic [19,20].

Representatives of Monilifera live on sunken wood, ropes, etc., although some species live on muddy substrates [21–25]. Moniliferans, according to some reports, have methane-oxidizing symbionts [13], but other studies confirm the presence of sulfide-oxidizing bacteria [16].

Species of the Frenulata group (Pogonophora sensu stricto) contain symbionts of various types. Thus, *Siboglinum fiordicum* Webb, 1963 and one undescribed species of frenulate from the Japanese trough have sulfide-oxidizing symbionts [26,27]. The presence of methane-oxidizing symbionts has been confirmed for one species of frenulate pogonophore (*Siboglinum poseidoni* Flügel & Langhof, 1983) [28], but a number of publications also indicate the possible presence of methane-oxidizing symbionts in several other species (*O. haakonmosbiensis*, *Siboglinum atlanticum* Southward & Southward, 1958, *Siboglinum ekmani* Jägersten, 1956) (see [1,15]). Contradictory data on the presence of methane- or sulfide-oxidizing symbionts were provided by studies on two species of the genus *Oligobrachia* (*Oligobrachia haakonmosbiensis* Smirnov, 2000 and *Oligobrachia mashikoi* Imajima, 1973) [14–16,29–31].

Importantly, regardless of the type of symbionts contained, siboglinids are a characteristic component of communities living at hydrocarbon seep sites. This is because, under reducing conditions, microbiological oxidation of methane occurs with the participation of sulfates. This yields high concentrations of hydrogen sulfide in the sediment. The generated hydrogen sulfide acts as an energy source for sulfide-oxidizing symbionts of siboglinids [32–36]. This explains why siboglinids bearing sulfide-oxidizing symbionts are confined to such hydrocarbon seep sites.

The Arctic seas are characterized by major deposits of oil, gas and gas hydrates [37–41] This leads to the assumption that the diversity of siboglinids is very high in the Arctic. Nonetheless, data on findings of siboglinids in the Arctic Ocean are still scarce. Only three species of siboglinids are known in the Barents Sea. Two species of frenulates (*N. murmanicum* and *O. haakonmosbiensis*) and one species of moniliferan (*S. contortum*) are known from the Barents Sea [24,42]. While *N. murmanicum* is widely distributed there, the two other species of siboglinids in the Barents Sea are known only from the Haakon Mosby Mud Volcano at the border between the Barents and Norwegian Seas [24,43]. *N. murmanicum* was first discovered by L.I. Moskalev in the Barents Sea in the collections of 1958 and 1959; it was the first known frenulate pogonophore for this basin and was initially identified as a representative of the genus *Diplobrachia* [44]. Specimens were found at several stations in the southern part of the Barents Sea near 70° N 40° E (see [44], Figure 1). The first finds stem from muddy soils at a depth of 170–300 m and a water temperature from -1.22 °C to 4.08 °C. Later, A.V. Ivanov recognized those worms as belonging to a new species and genus of frenulates and provided a full zoological description without, however, discussing its distribution [42]. Ivanov later published more specific data on the geographic and bathymetric distribution in a monograph [45]. Accordingly, the species resulted to inhabit the Barents Sea at various latitudes (69°–75° NN; 35°–40° EE) and depths (170–325 m), but the coordinates of specific stations were not detailed [45]. Subsequently, *N. murmanicum* was found several more times in the Barents Sea, but all the sites fell within the abovementioned area [46]. The literature also points to findings of *N. murmanicum* in the Norwegian Sea [47,48].

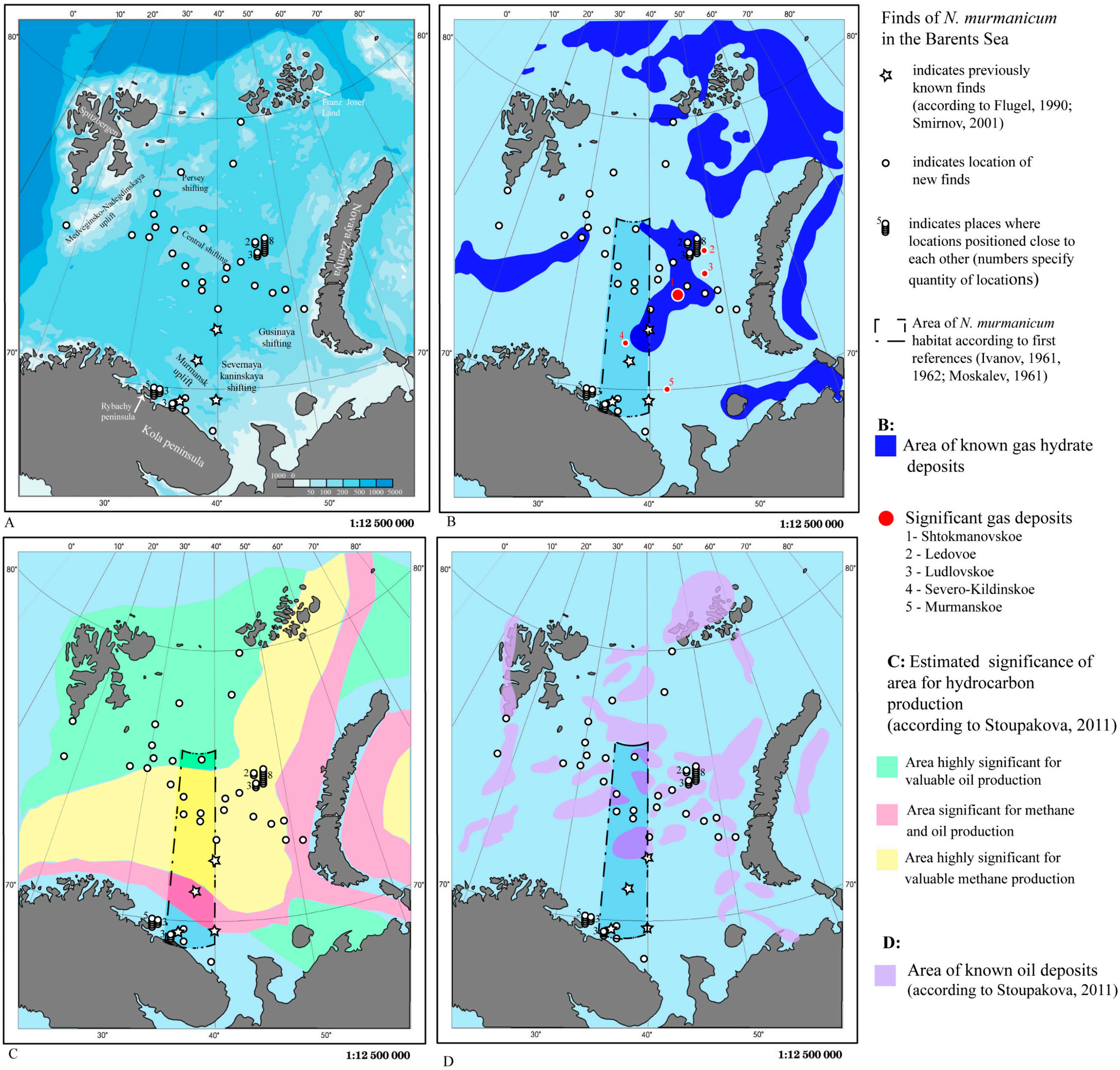

Figure 1. Distribution of *Nereilinum murmanicum* in the Barents Sea. (**A**)—physical map of the Barents Sea, (**B**)—gas hydrate deposits and most significant gas deposits, (**C**)—estimated significance of the area for hydrocarbon production (according to Stupakova, 2011), (**D**)—area of known oil deposits (according to Stupakova, 2011).

2. Materials and Methods

In this paper, we report previously unpublished data on the distribution of *N. murmanicum* in the Barents Sea based on new findings made during the period from 1993 to 2019. Frenulates were collected during cruises of the research vessels "*Dalnie Zelentcy*" in 1993, "*Romuald Muklevich*" in 2003, "*Fridtjof Nansen*" in 2005, 2006, "*Smolensk*" in 2006, "*Vilnius*" in 2007, 2018, 2019, "*Professor Boyko*" in 2008 and 2011, R/V "*Academik Treshnikov*" in 2019 and R/V "*Professor Levanidov*" in 2020. In all cruises, the material was collected using a 0.1 m^2 Van Veen grab. The bottom grab samples were washed in a gas conical washing sieve with a mesh size of 0.75 mm.

The samples yielded adult and juvenile individuals, empty tubes, and tubes in which embryos and larvae were found in addition to adults. All samples werefixed in 4% formalin on the filtered seawater. *N. murmanicum* adult individuals in tubes, larvae and embryos were collected at 53 locations (in cases when several stations were located very close to each other, they were combined and counted as one location) at depths of 75.2–375 m (Table 1).

Table 1. Data on newly collected material of *Nereilinum murmanicum* in the Barents Sea from 1993–2020. (A—adults, E—embryos, J—juveniles, L—larvae, T—empty tubes).

R/V	Stations	NN	EE	Date	Depth, m	Temp., °C	Salinity	Sediment	Material
R/V *Vilnius*	37	69.05	39.71	8 August 2007	226.7			Silt	A, T
R/V *Dalnie Zelentcy*	36	69.21	35.96	26 June 1993	195			Sand	A
R/V *Dalnie Zelentcy*	34	69.43	37.21	24 June 1993	185				A
R/V *Professor Boyko*	2011-5	69.48	35.21	8 July 2011	175.5			Sand	T
R/V *Professor Boyko*	38	69.51	36.00	27 June 1993	200				A
R/V *Romuald Muklevich*	23-2	69.53	32.88	12 August 2003	254	3.08	34.489	Silt	A
R/V *Professor Boyko*	C-1	69.55	32.59	5 July 2011	204			Sand	A, J, L
R/V *Romuald Muklevich*	22-1	69.55	32.87	11 August 2003	224.8	2.9	34.451	Silt	A, E, L, T
R/V *Romuald Muklevich*	19-1	69.55	32.59	11 August2003	204	4.76			A, T
R/V *Romuald Muklevich*	20-4	69.56	32.65	11 August 2003	241.8	2.76	34.418	Silt	A, L, T
R/V *Romuald Muklevich*	27-2	69.58	33.10	13 August 2003	225.6	3.12	34.501	Silt	A
R/V *Romuald Muklevich*	28-1	69.59	33.15	13 August 2003	232.6	2.94	34.451	Silt	A
R/V *Professor Boyko*	15-1	69.59	36.34	23 November 2008	190.3	3.49	34.599	Silt	A, L
R/V *Dalnie Zelentcy*	32	69.67	40.00	24 June 1993	170			Sand	A
R/V *Fridtjof Nansen*	43-2	72.30	40.00	28 September 2006	341	0.15	34.99	Silt	A, E, T
R/V *Smolensk*	23-5	72.30	51.01	11 September2006	75.2	0.11	34.73	Stones	A
R/V *Smolensk*	19-3	72.30	48.60	7 September2006	175.2	2.98	34.49	Silt	A, T
R/V *Fridtjof Nansen*	44-2	72.99	38.01	28 June 2006	237	0.63	35.03	Sand	A, E, L, T
R/V *Smolensk*	21-1	73.00	47.02	10 September2006	312.6	−0.12	34.96	Clay	A, T
R/V *Smolensk*	22-3	73.00	49.02	10 September2006	243.7	1.93	34.99	Clay	A, T
R/V *Smolensk*	33	73.30	35.59	25 Septembe 2006	261			Silt	T
R/V *Smolensk*	25-3	73.30	45.10	12 September2006	321.5	−0.31	34.96	Clay	A, E, T
R/V *Smolensk*	34-2	73.30	38.03	25 September 2006	263.5			Clay	A, T
R/V *Professor Levanidov*	D2	73.58	41.33	7 August 2020	275			Clay	A, T
R/V *Vilnius*	51	73.97	41.54	24 October2018	274	0.15	34.964	Silt	A
R/V *Smolensk*	32-3	74.00	35.60	24 September2006	228.9			Silt	A, T
R/V *Vilnius*	Lud15	74.36	45.99	10 July 2019	287				A, L, T
R/V *Professor Levanidov*	Lud15	74.22	43.38	30 July 2020	289			Clay	A, T
R/V *Vilnius*	6	74.36	46.01	17 October 2018	286	1.62	34.964	Silt	A, L, T
R/V *Professor Levanidov*	Lud6	74.44	45.59	1 August 2020	292			Clay	A, E, T
R/V *Vilnius*	Lud10	74.48	45.64	9 July 2019	306				A
R/V *Professor Levanidov*	Lud7	74.49	46.38	2 August 2020	221			Clay	A, E, L, T
R/V *Fridtjof Nansen*	12-1	74.50	33.48	2 September 2006	257.6	0.08	35.03	Silt	A, J, T
R/V *Professor Levanidov*	Lud2	74.52	45.35	2 August 2020	291			Clay	A
R/V *Professor Levanidov*	Lud3	74.58	46.16	2 August 2020	270			Clay	A, E, T
R/V *Vilnius*	Lud6	74.72	45.95	9 July 2019	297				A, T
R/V *Vilnius*	17	74.73	45.98	18 October 2018	296	1.55	34.956	Silt	A, T
R/V *Vilnius*	Lud7	74.82	46.65	8 July 2019	222				T
R/V *Vilnius*	18	74.83	46.66	18 October 2018	221	1.45	34.883	Silt	A, L, T
R/V *Fridtjof Nansen*	6-4	74.83	17.44	29 August 2006	296.4	4.43	35.065	Silt	T
R/V *Vilnius*	22	74.97	45.26	18 October 2018	269	1.45	34.908	Silt	A, L, T
R/V *Vilnius*	3	74.97	46.25	8 July 2019	279				A, L, T
R/V *Fridtjof Nansen*	16-5	75.00	29.90	4 September 2006	375.3	1.35	35.06	Sand	A
R/V *Fridtjof Nansen*	60-5	75.01	27.48	5 October 2005	311.4	1.58	35.05	Silt	T
R/V *Fridtjof Nansen*	15-2	75.50	30.48	4 September 2006	367.1	1.27	35.06	Silt	T
R/V *Fridtjof Nansen*	14-1	75.50	33.49	3 September2006	223.1	1.30	35.07	Sand	A, E
R/V *Smolensk*	27	75.60	38.01	23 September2006	248.1			Clay	T
R/V *Fridtjof Nansen*	18-4	75.86	29.93	6 September2006	303.2	1.88	35.07	Sand	A, T
R/V *Fridtjof Nansen*	5-1	76.06	16.25	28 August 2006	364.6	2.61	35.01	Silt	A
R/V *Fridtjof Nansen*	21-2	76.61	30.00	8 September 2006	282.6	2.05	35.07	Sand	A, T
R/V *Fridtjof Nansen*	24-4	77.51	33.54	8 September2006	150.9	1.81	34.94	Sand	A
R/V *Fridtjof Nansen*	35-3	78.03	43.00	15 September2006	267.6	0.05	34.99	Sand	A, L, T
R/V *Academik Treshnikov*	39B	79.63	44.72	6 May 2019	126				A

Observations of specimens for species identification were made using a stereomicroscope Olympus SZX-ZB7 (Olympus Corp., Tokyo, Japan).

Data on temperature and salinity of the water bottom layer were received by CTD-probe Mark 3B (Falmouth Scientific, Inc., Pocasset, MA, USA) at 30 of the stations (Table 1). The granulometric sediment composition was determined at 44 stations, whereby this work considers only the dominant granulometric fraction. The method used for grain size determination is wet sieving (method ISO 11277:2009, applied to fractions above 63 µm).

The maps were constructed using Surfer v 22 (Golden Software, Golden, CO, USA) for the Barents Sea region bounded in the west and east by longitudes of 10° E and 60° E, in the south and north—at latitudes 67° N and 80° N. Maps using for final illustration were additionally edited in Adobe Photoshop and Adobe Illustrator (Adobe Inc., San Jose, CA, USA).

Diagrams of distribution of stations in relation to abiotic environmental factors were built using standard tools of Microsoft Excel 365 (Microsoft Corp., Redmond, WA, USA).

3. Results

We analyzed collections of frenulates from 53 stations sampled in the Barents Sea (Table 1). In total, 310 juveniles and adult individuals, 128 embryos, and 177 larvae of a frenulate *Nereilinum murmanicum* were discovered at 46 stations in different parts of the Barents Sea. Empty tubes that are identical to those of *N. murmanicum* were recorded at 35 stations. At seven stations only empty tubes were sampled (Table 1). The embryos were found in nine tubes of *N. murmanicum* sampled between June and September. Tubeworm females that were brooding embryos were present at nine different stations (Table 1). Larval stages were found in tubes of 22 adults of *N. murmanicum* sampled from June to November. In total, individuals with larval stages in tubes were found at 12 stations (Table 1).

3.1. Geographical and Bathymetric Distribution

The findings of the adults and empty tubes of *N. murmanicum* were distributed over a large area of the Barents Sea basin. Adult and juvenile *N. murmanicum* were collected at the depth range from 75.2 to 375.3 m. We present here the map with the updated species distribution in the Barents Sea from the northernmost to the southernmost latitudes as well as from the easternmost to the westernmost longitudes (Figure 1). This area bounded by 69.05–79.63 NN, and 16.25–51.01 EE.

Most of the findings were detected in the central part of the Barents Sea basin and along the coast of the Kola Peninsula. With respect to the central part of the basin, most findings were from the Central shifting and along its periphery, especially in the area east of the Central shifting. In this area, *N. murmanicum* individuals were discovered at 13 stations. A total of 82 adults and juveniles of *N. murmanicum* were found at these stations. Importantly, two stations within this area yielded the highest numbers of individuals per grab: 34 specimens (R/V *Vilnius*, station #18, 74.83 NN, 46.66 EE) and 25 individuals (R/V *Vilnius*, station #22, 74.97 NN, 45.26 EE). In the Kola Peninsula area, a large part of the findings were concentrated to the east of the Rybachy Peninsula in the Motovsky Bay. There, we recorded *N. murmanicum* at eight stations.

The northernmost finding of *N. murmanicum* available to us stems from the southwest of the Franz Josef Land archipelago. Two adult *N. murmanicum* were found at this station at a depth of 126 m. The southernmost finding was off the coast of the Kola Peninsula. Only one specimen of *N. murmanicum* was recorded there.

Juveniles were recorded at two stations: to the west of the Central shifting at a depth of 257.6 m and in the area of the Rybachy Peninsula off the coast of the Kola Peninsula at a depth of 204 m.

Embryos were found in the adult tubes from two stations: in the region of the Rybachy Peninsula in Motovsky Bay, and at seven stations located to the south, southeast, and west of the Central Barents Sea. Those embryos stem from depth ranges of 204–341 m.

Larval stages were found in the adult tubes at three stations in the Motovsky Bay: one station off the coast of the Kola Peninsula, specifically east of the Motovsky Bay, seven stations to the south and east of the Central shifting, and a station east of the Persey shifting. Larval stages were found at depths of 190–287 m.

Empty tubes were recovered at more than the half of all stations (35), including seven stations at which only empty tubes were collected and no other material related to *N. murmanicum* was found. Stations with only empty tubes were encountered south of Spitsbergen (single station), all around the Central shifting and off the coast of the Kola Peninsula at depths of 175–367 m.

3.2. Relation of Distribution to Abiotic Factors

For the listed collections, we compared the data on the abiotic factors of the habitats of *N. murmanicum*, including temperature, salinity, and the granulometric composition of the sediment.

Temperature of the bottom water in the areas of the tubeworm habitats was obtained at 30 out of 53 stations. *N. murmanicum* temperature ranges were from −0.31 to 4.76 °C. The distribution of stations by temperature values was as follows: two stations featured values < 0 °C; six stations were in the range from 0 to 1 °C, eleven stations in the range from 1 to 2 °C, six stations in the range from 2 to 3 °C, (Figure 2). Two stations with the coldest bottom water temperatures (<0 °C) were located to the south and southeast of the Central shifting and were measured in September 2006. The warmest water stations were located in different regions: one was to the south of Spitsbergen in the area of the Medvezhinsko-Nadezhdinskaya uplift (4.43 °C in August 2006), another was in the Motovsky Bay (4.76 °C in August 2003). Individuals with larvae in tubes were found in a wide temperature range, from 0.05 to 3.49 °C. Embryos were present at those stations with a sediment temperature from −0.31 to 2.9 °C.

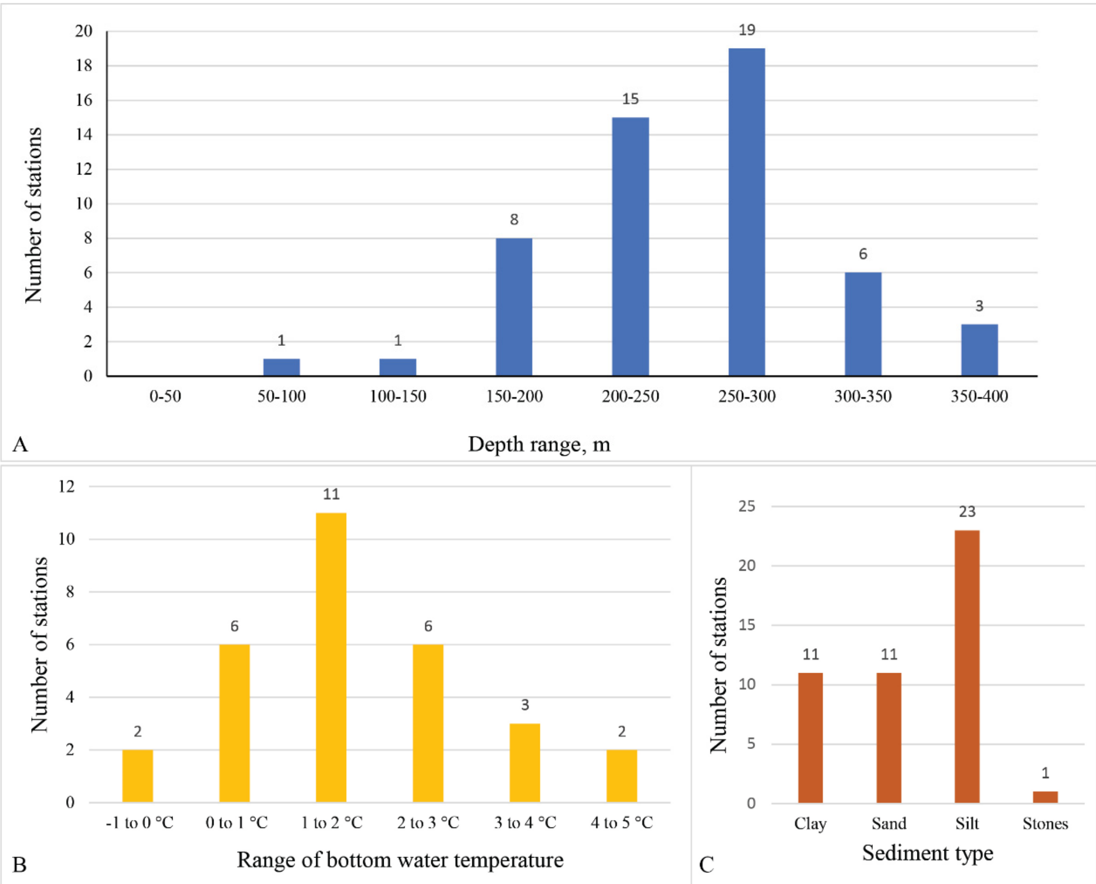

Figure 2. Distribution of stations with new finds of *Nereilinum murmanicum* in relation to abiotic environmental factors. (**A**)—distribution of stations by depth, (**B**)—distribution of stations by bottom water temperature, (**C**)—distribution of stations by sediment type.

All the records of frenulates in the Barents Sea were associated with salinities in a very narrow range, from 34.42 to 35.07. The station with the highest salinity overlapped with one of the stations with the highest temperatures, which were located south of Spitsbergen in the area of the Medvezhinsko-Nadezhdinskaya uplift. Only empty tubes of *N. murmanicum* were found at this station. The lowest salinity was recorded at one of the stations in the

Motovsky Bay. Individuals with larvae and embryos in tubes were detected at the stations with salinity ranges from 34.45 to 35.03.

According to the granulometric composition, we subdivided all stations into four categories according to the main granulometric component of sediments: silt (23 stations), sand (11 stations), clay (11 stations), and "stones" (rocky ground, one station) (Figure 2). In the category "silt" we included silt, clayey silt, sandy and fine sandy silt. The category "sand" included sand, silty sand with stones and gravel, silty sand with clay and gravel. Clay and silty clay as well as clay with coarse sand were assigned to the category "clay".

At the large majority of stations (45), the number of adult specimens per station was less than 10. At 39 of these stations, no more than three specimens were collected per station. Two of the stations from the east side of the Central shifting yielded the highest numbers of individuals per grab: 34 (R/V *Vilnius*, station #18, 74.83 NN, 46.66 EE) and 25 (R/V *Vilnius*, station #22, 74.97 NN, 45.26 EE). At these stations the following abiotic factors were recorded in October 2018. At station #18, the specimens were sampled at a depth of 221 m, in the silty sediment, a bottom water temperature of 1.45 °C and a salinity of 34.88. At station #22, the tubeworms were collected from 269 m (silty sediment, bottom water temperature 1.45 °C, salinity 34.90). In addition to adults, larvae and empty tubes were also found at these stations.

The maximum number of specimens per station is 36 adults. Two stations yielded this number of specimens from the studied collections in the Barents Sea. The first station was located to the west of the Central shifting (R/V *Fridtjof Nansen*, station #12, 74.5 NN, 33.48 EE). The tubeworms were collected from silty sediment at a depth of 257.6 m in September 2006. The bottom water temperature was 0.08 °C, salinity 35.03. The 36 individuals reflect the sediment content of four grabs. In addition to adults, juveniles and empty tubes were collected at the station. The second station was located in the Motovsky Bay (R/V *Romuald Muklevich*, station #22, 69.55 NN, 32.87 EE). At this station, the material was collected from silty sediment at 224.8 m; at the season of collection, August 2003, the bottom water temperature was 2.9 °C, salinity 34.45. The 36 individuals reflect the examination of sediment from five grabs. In addition to adults, empty tubes were present at this station.

4. Discussion

4.1. Geographical and Bathymetric Distribution

The new findings considerably expand the known range of *N. murmanicum*. In the Barents Sea, this species was found within the area bounded by 69.05–79.63 NN, and 16.25–51.01 EE (Figure 1). The northern boundary of the *N. murmanicum* habitat is the south-eastern part of the Persey shifting. From the west, the area is limited by the Medvezhinsko-Nadezhdinskaya uplift on the border of the Barents and Norwegian Seas. The southernmost findings approach the coast of the Kola Peninsula. In the east, the range is limited by the Central Depression and the south-eastern coast of Juzhnyi Island in the Novaya Zemlya archipelago. The depth range at which *N. murmanicum* was found is 75.2–375.3 m. Most of the findings (81%) were made at depths between 200 and 350 m (Figure 2A). Other findings surround the Central shifting at depths <200 m and are located to the east and west of the Spitzbergen's shifting at depths <100 m. The findings in the southern part of the Barents Sea are confined to the trough between the coast and the Murmansk uplift. Note that the findings of *N. murmanicum* in the Norwegian Sea were made at significantly greater depths, i.e., 1300 m [47,48].

4.2. Environment

All the finds where the sediment composition was recorded except one are confined to soft sediments (silt, silted sand, clay), and 72% of those finds are confined to sandy and silty sediments (Figure 2C). Frenulate tubes are positioned vertically or almost vertically in the substrate [26,49,50]. As the frenulates grow, they sink into the sediment, burying themselves with the help of an opisthosome, which protrudes through the lower open end of the tube [22,51]. Accordingly, stony substrates are unsuitable for frenulate settlement:

only one finding of *N. murmanicum* was on a stony substrate. Dense clays can hinder the diffusion of fluids containing dissolved gases. Such gases, however, are necessary for the vital activity of symbionts. In our material, 11 finds (25%) are confined to clay-containing sediments (Figure 2C).

The Barents Sea is characterized by low bottom water temperatures, and most of the findings (83%) are associated with temperatures below 3 °C (Figure 2B). Siboglinids are not found in desalinated areas of the world oceans. At first glance, this pattern appears to be violated by the presence of *Crispabrachia yenisei* and *Galathealinum karaense* in the Yenisey Bay in the estuary area of the great Siberian Yenisey River [52,53]. However, this area is characterized by strongly stratified waters: at a depth of 28 m, where frenulates were collected, the salinity approaches that of oceanic values [54]. All the records of frenulates in the Barents Sea are associated with salinities in a narrow range from 34.42 to 35.07.

The new findings significantly expand the range of *N. murmanicum* in the Barents Sea. Together with previously known locations, records are now available from 58 locations. Interestingly, most of the findings (43 locations or 74%) fall in areas known as highly promising for oil and gas production (Figure 1C). Twenty-eight locations (48%) are associated with areas of known oil deposits, and 22 locations (37%) are associated with areas explored for gas hydrate deposits (Figure 1B,D). *N. murmanicum* was also found near the largest gas fields in the Barents Sea, namely Shtokman, Ludlovskoye and Ledovoye (Figure 1B).

4.3. General Connection of Siboglinids Findings to Hydrocarbons

Siboglinids are quite often confined to areas of hydrocarbon seeps. Thus, cold seep vestimentiferans—representatives of the genera *Lamellibrachia*, *Seepiophila* and *Escarpia*—reach high numbers around hydrocarbon seeps in the Gulf of Mexico and on the slope off Louisiana [55–63]. This pattern is also valid for siboglinids of the subfamilies Frenulata and Monilifera [16,31,48,64–77].

The Arctic has enormous oil and gas reserves [78]. According to the United States Geological Survey, at least 13% of the world's undiscovered oil reserves and at least 30% of the world's undiscovered gas reserves are located above the Arctic circle, most offshore at depths <500 m [37–39]. Among the Russian Arctic seas, the Barents Sea and the Kara Sea are the most promising regions in terms of oil and especially gas production. Two-thirds of the undiscovered gas reserves in the Arctic are presumably located in four regions: South Kara Sea, South Barents Basin, North Barents Basin, and the Alaska Platform [37,38]. The geological structure of the Barents Sea shows great promise for large hydrocarbon reserves [79–91]. Several of the richest deposits have been discovered in the Russian part of the Barents Sea, including the Shtokmanovskoe (Shtokman), Ledovoe, Ludlovskoe, Murmanskoe, and Severo-Kildinskoye fields, with total gas reserves of at least 4.4 trillion m^3. A major part of the reserves falls on the Shtokmanovskoe field, containing, according to Gazprom Corporation, at least 3.9 trillion m^3 of gas and 39 million tons of gas condensate [92].

High concentrations of hydrocarbons in the sediments of the Arctic basin seas suggest the presence of a rich siboglinid fauna. In recent years, significant progress has been made in the study of Arctic Sea siboglinids. Eleven species of frenulate pogonophorans belonging to 7 genera are known in the basin of the Arctic Ocean along with its border seas (*Crispabrachia yenisey* Karaseva, Rimskaya-Korsakova, Ekimova, 2021, *Galathealinum arcticum* Southward, 1962, *Galathealinum karaense* Smirnov, Zaitseva & Vedenin, 2020, *Siboglinum ekmani*, *Siboglinum hyperboreum* Ivanov, 1960, *Siboglinum norvegicum* Ivanov, 1960, *Nerelinum murmanicum* Ivanov, 1961, *Nereilinum squamosum* Smirnov, 1999, *Oligobrachia haakonmosbiensis*, *Polybrachia gorbunovi* (Ivanov, 1949), *Polarsternium rugellosum* Smirnov, 1999 [24,42,45,46,52,53,93–96]. Moreover, the moniliferan *Sclerolinum contortum* Smirnov, 2000, known for its bipolar distribution, is found in this region [43]. The most diverse fauna of frenulate pogonoforans in the Arctic region is described from the Laptev Sea (*N. squamosum*, *O.* cf. *haakonmosbiensis*, *Pol. gorbunovi*, *P. rugellosum*, *S. hyperboreum*) and the Central basin (*S. ekmani*, *S. hyperboreum*, *S. norvegicum*, *N. squamosum*, *O. haakonmosbiensis*) [24,45,46,93–96]. Very recently, two new species were described close to each other in the Kara Sea in the area of Yenisey River estuary (*C. yenisey*, *G. karaensis*) [52,53]. One species has been described (in the sense found) in the East Siberian (*O.* cf. *haakonmosbiensis*) [97] and Greenland (*S. hyperboreum*) [46] seas and another one in the Beaufort Sea (*G. arcticum*) [94]. Representatives of the genus *Oligobrachia* have also been reported in the Beaufort Sea, exhibiting a high similarity in 18S-RNA c to *O. haakonmosbiensis*; they also have symbionts closely related to *O. haakonmosbiensis* symbionts from the Barents Sea and the Laptev Sea [98]. Thus, among Arctic marginal seas, the Chukchi Sea is the only one lacking any frenulate (or siboglinid) species.

Many of the siboglinid findings in the seas of the Arctic basin were associated with high concentrations of hydrocarbons [52,53,74,76,97,99]. Recent studies have shown that *Oligobrachia* is a reliable indicator of methane seeps in the Laptev Sea [31,76,77,100]. Currently, only very few findings of frenulate siboglinid worms are available from the Kara Sea [52,53]. They are confined to the estuarine areas of the Yenisei River, where increased methane concentrations are probably associated with the result of the degradation of permafrost strata under the influence of river runoff [101,102]. Given the high hydrocarbon potential of the Kara Sea (see [37,38,82]), we expect a much wider distribution of siboglinids in this sea. Frenulate *Oligobrachia* and moniliferan *Sclerolinum* form high-density populations at the underwater mud volcano Haakon Mosby in the Norwegian Sea [67,68]. Frenulate siboglinids in several areas of the North Atlantic also prefer sediments with a higher methane concentration [48]. The frenulate worm *S. poseidoni*, for which the presence of methane-oxidizing symbionts has been reliably established, was detected at high methane concentrations in the sediment: 3.4×10^6 nmol/L in the Skagerrak Strait [103] and 5.5×10^6 nmol/L around the underwater mud volcano Captain Arutyunov (Gulf of Cadiz) [70]. Six species of frenulate worms are reported in the Sea of Okhotsk [45,93,104–106], confined mostly to areas where the sediment methane concentration varies between 0.22 and 4.46×10^9 nmol/kg, whereas areas with normal background concentrations were comparatively rarely inhabited [107,108]. Moniliferan *Sclerolinum* was found in Antarctica near Hook Ridge along the Antarctic Peninsula at methane concentrations of 26×10^3 nmol/L [66,72].

5. Conclusions

The first representative of Siboglinidae was found in seas close to the Sunda Archipelago in 1914 [109]. Over the next several decades, siboglinids were found in all oceans [23,24,45,93–95,104,105,110–119]. While the feeding mechanism of the frenulate pogonophorans was not discovered until 1980 [120–122], the authors describing new species of frenulates from different regions of the World Ocean had no idea about the association of pogonophorans with hydrocarbon seeps and never linked their findings with areas of high concentrations of hydrocarbons. Later, it became clear that some frenulates inhabit locations within areas of underwater deposits of oil and gas, for example the Gulf of Mexico, the Norwegian Sea, and the Barents Sea [23,24,42,112]. The example of the Sea of Okhotsk is very indicative. In the 1950s–1960s, the Soviet expeditions, yielded numerous findings of frenulates in the Sea of Okhotsk [105,123–126]. At that time, however, there was no evidence of symbiotrophic feeding of frenulates. Later, it was revealed that frenulate finds in the Sea of Okhotsk overlap with areas of high hydrocarbon concentrations in the sediment and bottom water [107,108].

There is still no information about the presence of hydrocarbon seeps in numerous areas of frenulate habitats in the World Ocean. The fact that the nutrition of frenulates relies on methane- or sulfide-oxidizing bacterial symbionts suggests that the locations inhabited by frenulates should coincide with hydrocarbon-rich regions. This makes frenulates indicator organisms: wherever frenulates are found, one should seek high methane concentrations (of any origin) there.

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review and editing—N.K., V.M., M.G. and N.R.-K.; visualization—N.K.; supervision—V.M.; project administration—M.G.; funding acquisition—V.M., N.K. and M.G. All authors have read and agreed to the published version of the manuscript.

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