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ORIGINAL PAPERS

Findings of Pogonophores (Annelida and Siboglinidae) in the Kara Sea Associated with the Regions of Dissociation of Seafloor and Cryogenic Gas Hydrates

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Abstract—The discovery of new occurrences of pogonophores *Siboglinum* sp. and *Nereilinum* sp. from the St. Anna Trough (northwestern portion of the Kara Sea) is described in this paper. Previously, occurrences of pogonophores (*Crispabrachia yenisey* and *Galathealinum karaense*) were reported in the southern part of the Kara Sea, in the estuary of the Yenisei River. Two areas in the Kara Sea where pogonophores were found coincide with the regions of distribution of two types of gas hydrates: oceanic seafloor gas hydrates, and gas hydrates associated with permafrost. Gas hydrate deposits in the permafrost are confined to the coastal regions of the Kara Sea. A methane flux forms in areas of dissociation of gas hydrates under the influence of river runoff. This methane source is vital for the survival of pogonophores. The existence of pogonophores in the St. Anna Trough indicates the presence of a methane flux associated with the inflow of Atlantic water, which causes dissociation of seafloor gas hydrates. The possible role of Arctic warming is apparent in both processes.

Keywords: pogonophores, gas hydrates, permafrost, Kara Sea, St. Anna Trough, Arctic warming, Siboglinidae
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INTRODUCTION

Siboglinids (*Siboglinidae*) are a family of sedentary annelids, all of whose representatives lack digestive tracts. The vital activity of siboglinids is provided by endosymbiotic bacteria. Four groups of organisms are distinguished within the *Siboglinidae*, differing in habitats and the type of symbiotic bacteria [34]. Heterotrophic endosymbionts of the genus *Osedax* obtain energy from the breakdown of lipids contained in the bones of cetaceans and large fish [30]. Vestimentiferans (*Vestimentifera*) have sulfide-oxidizing symbionts [21, 26]. *Monilifera* have methane-oxidizing or sulfide-oxidizing symbionts [59]. Species of the *Frenulata* group (*Pogonophora* sensu stricto), are known to have both methane-oxidizing and sulfide-oxidizing symbionts [52, 57]. It should be noted that free-living prokaryotes perform the oxidation of methane using sulfates in the sediment under reducing conditions, resulting in high concentrations of hydrogen sulfide, which serves as an energy source for sulfide-oxidizing symbionts [15, 16, 20, 35]. Thus, siboglinids with chemoautotrophic symbionts (except vestimentifera from hydrothermal vents) are usually associated with areas of hydrocarbon seeps in the World Ocean, regardless of whether they contain methane-oxidizing or sulfide-oxidizing bacteria.

Pogonophores have been not known to occur in the Kara Sea. Only recently, in 2020, two new species of pogonophorans were found in Yenisei Bay of the Kara Sea [36, 55]. The latest finds of pogonophorans in the Kara Sea make it possible to analyze the association of siboglinids with areas of gas hydrate deposits of various origins.

MATERIALS AND METHODS

During hydrobiological work on the 86th cruise of the research vessel *Akademik Mstislav Keldysh* in 2021, siboglinids were found at two stations located north of Cape Zhelaniya in the St. Anna Trough (northwest side of Kara Sea) (Fig. 1). The station coordinates, depths, and date of collection are given in Table 1. Temperature and salinity data were computed on an SBE 21 SEACAT thermosalinograph (Sea-Bird Elec-

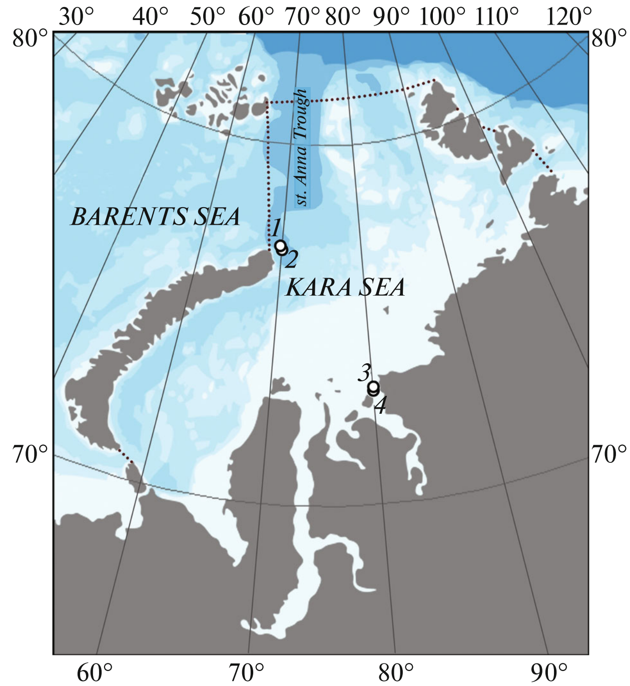

Fig. 1. Finds of pogonophores in the Kara Sea: (*1*, *2*), in the St. Anna Trough; (*3, 4*), in the Yenisei Bay. The dotted line shows the geographic boundaries of the Kara Sea.

tronics, Inc.). The method for processing data on depth, temperature, and salinity during this voyage has been described separately [44]. Sediments were sampled using an "Okean" bottom grab with an 0.25 m^2 aperture. After raising the bottom grab onto the deck, sediment samples were washed through a sieve with 0.15-mm mesh size. Samples were studied under Mikmed (Russia) and Olympus SZX (Japan) stereo microscopes. Live organisms were photographed using a LabCam eyepiece (iDuOptics, United States) for a 6S Iphone (Apple, United States). The residue was fixed in 96% ethanol. At station 7249 (539-m water depth), three siboglinid tubes were found, two of which contained live worms. At station 7250 (437-m water depth) two empty siboglinid tubes were found. At the present time, it is not possible to reliably identify these specimens to the species level, due to the insufficiency of the material. Therefore, we restrict ourselves to a generic identification.

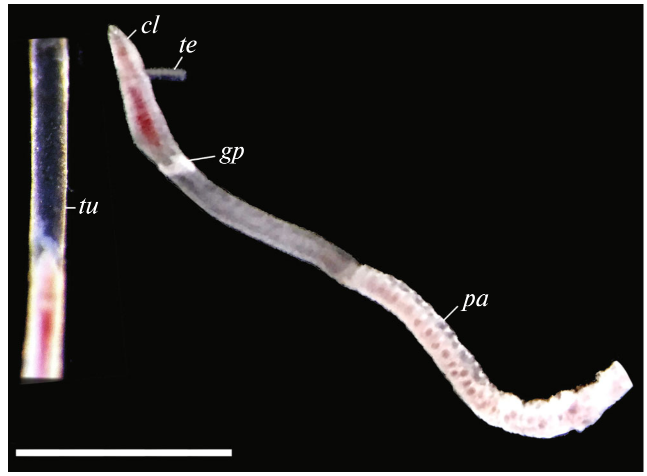

Fig. 2. A pogonophora *Siboglinum* sp. from the St. Anne's Trough. Designations: *cl*, cephalon lobe; *gp*, glandular spots; *pa*, papillae; *te*, tentacle; *tu*, tube. Scale: 1 mm.

RESULTS

The specimens belong to two unidentified species of two genera: *Siboglinum* and *Nereilinum*.

Siboglinum sp. A single specimen was found in a sample obtained at station 7249. The tube, 18 cm long and about 0.2 mm in diameter, is translucent, whitish-yellow, without annulation along its entire length (Fig. 2, *tu*). The tube contains a fragment of a 6-cm long worm. The cephalon lobe is conical (Fig. 2, *cl*). There is a single tentacle (Fig. 2, *te*). A white glandular band is clearly visible behind the frenulum (bridle) (Fig. 2, *gp*). The metameric part of the preannular part of the body bears two rows of dorsal papillae (Fig. 2, *pa*). In terms of morphological features, this specimen differs from most known species of the genus *Siboglinum* in the structure of the tube, which is completely devoid of annulation.

Nereilinum sp. The material includes two tubes in the sample taken at station 7249 and two tubes in the sample from station 7250. The tubes are up to 17-cm long and 0.15–0.2 mm in diameter. The tubes have distinct annulation (Fig. 3, *tu*). A fragment of a 5-cm long worm was found in one of the tubes from a sample obtained at the station 7249. The cephalon lobe is short and sharply conical (Fig. 3, *cl*), there are two tentacles (Fig. 3, *te*) and a groove in front of the frenulum, which is in contact with it on the ventral side.

Table 1. The locations of the stations in the St. Anne's Trough where pogonophores have been found

Station No	Northern Latitude	Eastern Longitude	Depth, m	Temperature, °C	Salinity, ‰	Collection date
7249	77.0001	70.0021	539	–0.9402	34.8310	Oct. 22, 2021
7250	77.4999	68.9953	437	–1.0171	34.8299	Oct. 22, 2021

The bridle is clear; below it there is a glandular band on the dorsal side, divided on the ventral side (Fig. 3, *br*, *gp*). On the dorsal side of the metameric part of the body, on slightly isolated papillae on each side of the dorsal groove, there are openings of tubiparous glands (Fig. 3, *pa*). Two larvae were found in the tube.

DISCUSSION

At the present time, Siboglinids are known only in two regions of the Kara Sea. One of these regions is Yenisei Bay in the southern part of the sea [7, 36, 55]. The discovery of siboglinids in this area, between Sibiryakov Island and the western coast of the Taimyr Peninsula, is of interest in several respects. The vast majority of species of the family *Siboglinidae* are deep-water organisms, but both occurrences in the Yenisei Bay were made at an unusually shallow depth. *Crispabrachia yenisey* was found at a depth of 28 m [7, 36], while *Galathealinum karaense* was found at a depth of 25 m [55]. Such shallow depths are not characteristic of siboglinids. Siboglinids are stenohaline organisms; they are not found in brackish waters of the World Ocean [4]. The Yenisei Bay is characterized by strong vertical salinity stratification [3, 29, 33]. The long-term average of surface salinity is less than 5‰ in the region between Sibiryakov Island and the western coast of the Taimyr Peninsula (where *C. yenisey* and *G. karaense* occur) [33]. Despite the strong freshening of surface waters, the long-term average salinity approaches 30‰ at a 10-m depth [3, 29]. The bottom water salinity in this area ranges from 30 to 32.5‰ [33]. Thus, the area where *C. yenisey* and *G. karaense* both occur are geographically part of the Yenisei River estuary. In fact, pogonophores exist here in salinity levels close to oceanic. The site of the *C. yenisey* and *G. karaense* occurrences is located in the area where the concentration of methane in the surface water layer reaches 130 nM, which is the maximum value for the southern part of the Kara Sea [14]. High methane concentrations in this case arise as a result of the degradation of permafrost gas hydrates under the influence of river runoff [14, 22, 31]. This process proceeds intensively against the background of the general warming of the Arctic in the estuaries of the Ob, Yenisei, and Lena Rivers and other large rivers of the Russian Arctic resulting in high concentrations of methane in the water and its release into the atmosphere [1, 8, 50, 53, 54].

Similar conditions exist in the delta of Mackenzie River of the Canadian Arctic, where colossal runoff causes the strongest decrease of salinity of the surface water layers of the Beaufort Sea [41]. In a similar manner to Yenisei Gulf, waters at the Mackenzie River mouth display a strong salinity stratification, which ranges from 1 to 10‰ at the surface layer, and exceeds 31‰ at a 20 m depth all year round [41]. The pogonophoran species *Galathealinum arcticum* Southward, 1962, which are closely related to *G. karaense*, was

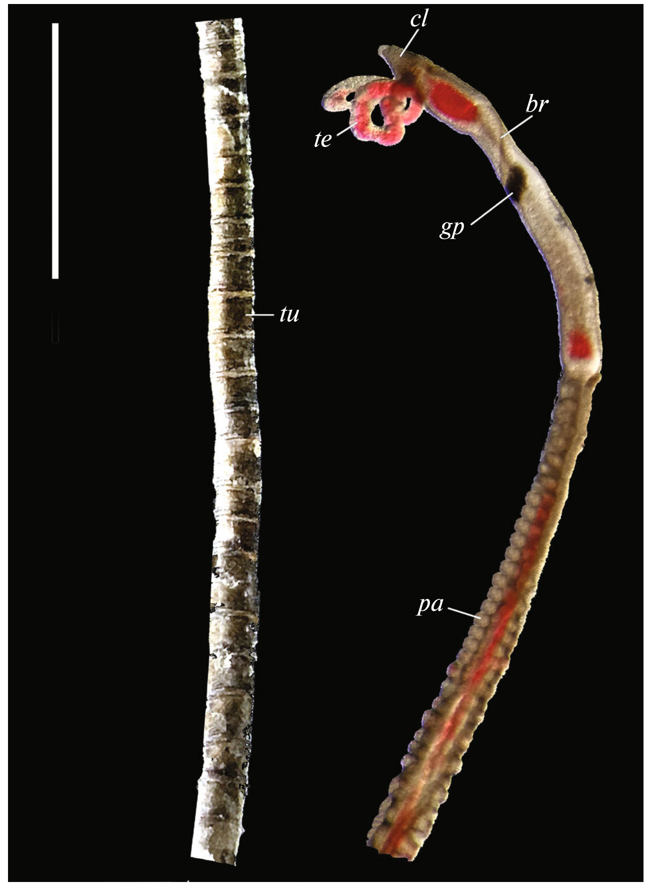

Fig. 3. A pogonophora *Nereilinum* sp. from the St. Anne's Trough. Designations: *br*, bridle, other designations as in Fig. 2. Scale: 1 mm.

found in the estuary area of the Mackenzie River at a depth of 36 m [56]. At the same time, the Mackenzie River delta and adjacent areas to the shelf of the Beaufort Sea are characterized by large deposits of gas hydrates in permafrost, which increasingly dissociate under the influence of river runoff resulting from global warming. These Arctic conditions generate powerful methane flows [17, 18, 42, 45, 46].

The seas of the Russian Arctic are considered to be a region of major hydrocarbon resources that exceed the potential reserves of all other Arctic countries [25, 28, 43, 58]. The Kara Sea surpasses other seas of the Russian Arctic in terms of hydrocarbon resources [5, 19]. It is known that the main reserves of hydrocarbons in the World Ocean are concentrated in the form of methane gas hydrates [2, 6, 11, 13, 23, 27, 37–39, 43, 47]. Gas hydrate deposits in the Russian Arctic are divided into two types. One of these is seafloor gas hydrates found at great depths in different regions of the World Ocean. The other type is gas hydrate deposits in the permafrost, which are typical for the marginal seas of the Russian Arctic. Seafloor gas hydrates occupy the deepwater regions of the Arctic Ocean, while gas hydrate deposits in the permafrost are

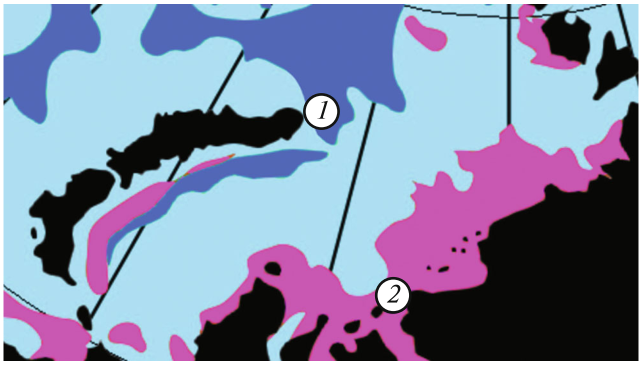

Fig. 4. Distribution of gas hydrates [9] and findings of pogonophores in the Kara Sea: (*1*), location of pogonophores in the St. Anna Trough; (*2*), in the Yenisei Bay. The area of gas hydrate deposits in the permafrost on the shelf is shown in pink, the area of seafloor gas hydrates is shown in blue.

located at shallow depths in relative proximity to the Russian Arctic coast [9, 10, 12, 13, 23, 43, 49, 53]. At the same time, the areas of seafloor deposits and permafrost gas hydrates in the Arctic seas are separated by vast zones where gas hydrates are absent either due to a lack of methane or due to the absence of thermobaric conditions necessary for the formation of clathrates [9, 10, 12, 49, 54].

Siboglinum sp. and *Nereilinum* sp. in the St. Anna Trough occur at depths greater than 400 m with salinities more than 34‰, which is quite typical for most pogonophores. Their habitat corresponds to the southernmost area of gas hydrate distribution in the St. Anna Trough [9, 10, 12]. It is known that climate warming in the Arctic leads to the dissociation of gas hydrates not only in the coastal zone, but also in deep-sea basins [32, 43, 48]. According to modeling results, almost complete dissociation of gas hydrates in the area of the St. Anna Trough is possible with a water temperature increase of only 2 degrees [32] (Fig. 5). Warm and salty Atlantic water flows through the Fram strait, into the central depression of the Arctic Ocean, and continues further along the St. Anna Trench and into the Kara Sea [24, 40, 44, 51]. Existing models [32] predict the dissociation of seafloor gas hydrates in this area and the resulting methane flux serves as a source that allows the metabolism of siboglinids living in the St. Anna Trough.

The two regions in which pogonophores were found in the Kara Sea are precisely the distribution areas of the two main forms of gas hydrates known in the Arctic (Fig. 4). The fauna of the siboglinids of the Arctic seas has been studied very poorly, but it is assumed that two groups of pogonophora species exist there. One group lives at shallow depths and is associated with gas hydrates in permafrost in the estuarine areas of large rivers and adjacent areas of the shelf. The other group occurs at the bathyal and abyssal depths typical of pogonophores and is associated with areas of dissociation of seafloor gas hydrates. Of course, this hypothesis should be considered as a purely preliminary one, it must be tested by further studies.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare no conflicts of interest.

Statement on the welfare of animals. All applicable international, national and/or institutional guidelines for the care and use of animals have been followed.

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