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Meiobenthos of the eastern shelf of the Kara Sea compared with the meiobenthos of other parts of the sea

Daria Portnova *, Alexander Polukhin

Shirshov Institute of Oceanology, Russian Academy of Sciences, 36 Nahimovskiy prospekt, 117997 Moscow, Russia

HIGHLIGHTS

- The meiobenthos is firstly studied in the eastern part of the Kara Sea shelf and 10 meiofaunal taxa were recorded.
- Meiobenthos from the eastern and central parts of the Kara Sea shelf and Yenisey estuary share taxonomic similarity.
- Abundance and diversity of meiobenthos affected by the hydrodynamics conditions, type of sediment and organic matter content.

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ABSTRACT

The meiofauna was studied at 7 stations in the eastern part of the Kara Sea shelf and at the southern edge of the Voronin Trough. The total meiofaunal abundance was 682 ± 403 ind./10 cm^2 and 10 major meiofaunal taxa were recorded for the eastern part of the Kara Sea. Canonical correspondence analysis indicated the depth, type of sediments and C_{org} content in the sediment as the main factors affecting the community structure. High taxonomic similarity was recorded for the meiobenthos of the eastern and central parts and the Yenisei River estuary. The meiobenthos abundance was significantly lower in the eastern part of the Kara Sea than in the central part and the Yenisei River estuary. The abundance and diversity of the meiobenthos are affected by the hydrodynamics, grain size, and organic matter content.

1. Introduction

The structure of coastal ocean ecosystems differs greatly among the continental shelves, being driven largely by differences in net primary production that are ultimately determined by the interplay of many factors such as boundary currents, shelf geometry, river runoff, upwelling and water and sediment chemistry that are unique to each shelf margin (Deubel et al., 2003). The most intense investigations in the Kara Sea, including the Ob and Yenisei estuaries, began in the 1990s. In the course of multi-year projects and marine field studies, a wealth of novel data has been collected, which considerably extended the information on the Arctic benthos and thus permitted testing the general validity of common notions about the structure and function of high-latitude benthic systems (Piepenburg, 2005). Sirenko (2001) listed a total of approximately 4800 macrobenthic species known for the entire Arctic, a total of 2895 known species for the Eurasian–Arctic shelf seas, and a total of approximately 400 known species for the deep Eurasian basins of the Arctic Ocean – a region that was almost unexplored 15 years ago but has recently been investigated in a number of studies. The Arctic shelf macro- and megafaunas have received more attention than the meiofaunal and microbial communities (Jørgensen et al., 1999; Piepenburg, 2005; Vedenin et al., 2015).

The meiofauna is an important component of benthic heterotrophic assemblages. The meiobenthos plays an important role in the remineralization of organic matter at the sea floor and changes the physical properties of sediments (Bessière et al., 2007). In terms of abundance and biomass, nematodes (Nematoda) and harpacticoids (Copepoda: Harpacticoida) typically dominate the meiofauna (Josefson et al., 2013).

The composition and distribution of meiobenthos in the Kara Sea were studied only in regard to the radioactive waste disposal along the eastern coast of the Novaya Zemlya archipelago from Abrosimov Bay to Stepovoi Bay (44–74 m) and in the area of the Novozemelskaya Depression (333–403 m) (Pogrebov et al., 1997; Galtsova et al., 2004). Particular attention was given to assessing the impact of radioactive contamination on the meiobenthic community (Galtsova and Alexeev, 2009; Alexeev and Galtsova, 2012). Garlitska and Azovsky (2016) provided data on the harpacticoids of Yenisei Gulf in the southern Kara Sea and discussed their distribution on the complex environmental gradients. An analysis of the species composition indicated the salinity, depth, type of sediments and chlorophyll a content in the water column as the main factors affecting the benthic harpacticoids (Garlitska and

* Corresponding author.
E-mail addresses: daria.portnova@gmail.com (D. Portnova), polukhin@ocean.ru (A. Polukhin).

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Azovsky, 2016). Portnova et al. (2017) reported the first data on the meiofaunal and nematode communities from the Yenisei Gulf and adjacent parts of the Kara Sea shelf. The data on meiofaunal and nematode species diversity confirm the lowest diversity observed in the freshwater and brackish water area (less than 5 psu) (Portnova et al., 2017). Harpacticoid and nematode assemblages do not form any particular brackish-water community but are segregated by depth, sediment type and water turbidity. The study in the Yenisei Gulf and adjacent parts of the Kara Sea demonstrates how the environmental conditions acting together affect the harpacticoid copepod and nematode community structures (Garlitska and Azovsky, 2016; Portnova et al., 2017). A similar zonation pattern caused by a set of conditions is typical for estuarine systems (Soetaert et al., 1995; Udalov et al., 2005; Alves et al., 2009; Semprucci et al., 2016).

This research aimed to extend meiofaunal studies within the framework of the multi-year programme of multidisciplinary investigations of the Kara Sea. The purpose of this study was to investigate the meiobenthos collected along a depth gradient transect (50–330 m) in the eastern part of the Kara Sea and in the southern part of the Voronin Trough. This study addresses the following questions. Do meiofauna densities and composition change along a bathymetric transect? Are these changes correlated with hydrophysical and hydro-chemical information available on the water column and sediment matrix? Is the distribution and abundance of the meiofauna along a depth gradient transect in the Eastern part of the Kara sea different than in other regions of the Kara Sea and other Arctic seas?

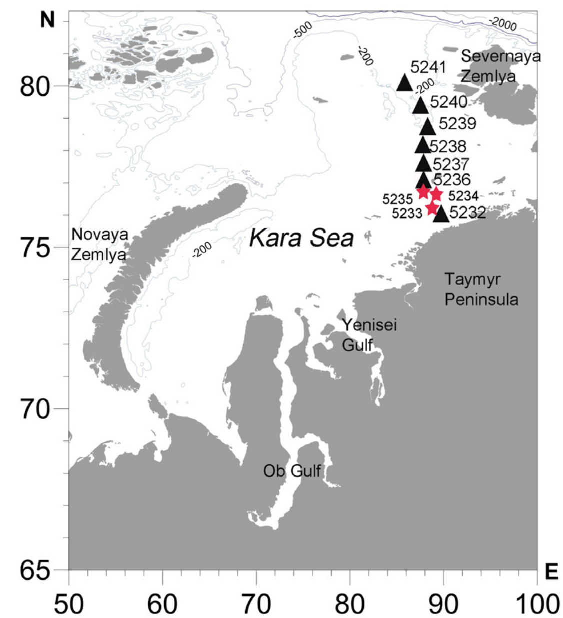

Fig. 1. Map of meiobenthic sampling sites in the Kara Sea. Red stars indicate additional hydrochemical stations 5233, 5234 and 5235 without meiobenthos sampling.

2. Material and methods

2.1. Study area

The Kara Sea, one of the Siberian shelf seas, extends up to 81°N, the eastern border with the Laptev Sea is at 100°E, and the western border is formed by the Novaya Zemlya archipelago (Pivovarov et al., 2003). The Kara Sea is shallow: its average depth is 110 m, with 40% of the area having depths less than 50 m. The sea bottom is relatively flat in the central part of the sea. A narrow strip 100 to 200 m deep extends from the coastal shallows to the north and forms the Central Kara Uplands (less than 50 m deep). Vize and Ushakov islands rise above this narrow strip. Two broad, deep trenches flank this upland, dividing the sea floor in the meridional direction. One of these trenches, the St. Anna Trough (620 m deep), extends to the east coast of Franz Josef Land for a distance of 150 km. The other, the Voronin Trough, which is 450 m deep, is located to the west of Pioneer Island (Severnaya Zemlya Archipelago) and at the same distance as the St. Anna Trough from Franz Josef Land. The sea is deeper in its western region, where the Novaya Zemlya Depression, with depths up to 420 m, stretches along Vaygach Island and the islands of Novaya Zemlya. In the southeastern part of the sea, the bathymetry is irregular, with numerous small depressions separated by ridges of varying height. Depths here range up to 100 m (Pavlov and Pfirman, 1995).

The shelf region of the Kara Sea is a link between the North Atlantic and the Arctic Oceans. The hydrography is characterized by frontal structures, transformation and mixing processes resulting from the penetration of warm and saline North Atlantic Water from the western boundary and abundant river runoff from the east (Makkaveev et al., 2017). Atlantic water comes to the Kara Sea in the north from the Barents Sea through the strait between Franz Josef Land and Novaya Zemlya. In the south, Atlantic waters (from the Barents Sea) extend eastward from the Kara Strait. As a result, relatively warm water of Atlantic origin penetrates into the Kara Sea through the St. Anna and Voronin troughs, and the water temperature increases at the 50–100 m depth, reaching maximum values of 1.0 °C to 1.5 °C (Dmitrienko et al., 2010). The investigated area includes the eastern part of the Kara Sea shelf, which spreads over a thousand kilometres from approximately 75°N to 80°N (Fig. 1).

The water temperature in the Kara Sea is quite low because of the ice covering the sea most of the year. The surface temperature decreases from southwest to northeast. In the northern part of the sea with drifting ice, the temperature in summer is only slightly higher than the freezing point. Ice formation begins in the Kara Sea in September in the north and in October in the south. Fast ice occupies the coastal zone and its development is patchy. Most of the fast ice in the river estuaries melts in place, although ice reconnaissance flights have observed river ice as far north as 80°N (Pavlov and Pfirman, 1995). The two largest Siberian rivers, the Ob and Yenisei, flow into the Kara Sea, causing a substantial decrease in salinity in the upper 20 m layer. These rivers' discharges exceed 40% of the total annual arctic river runoff (Galimov et al., 2006). The central and eastern parts of the Kara Sea are dominated by the Ob and Yenisei estuaries (= the Yamal Plateau) with a characteristic depth of 25 to 30 m. The regional pattern is a result of the cyclonic circulation driven by the prevailing winds, with river runoff discharged in the southern Kara Sea, and a southward flow of shelf water in the west. Due to high river runoff, Kara Sea waters have salinities from < 10 in the south to approximately 35 psu in the north (Pavlov and Pfirman, 1995).

The investigated area is influenced by the Yenisei River (Fig. 2) (Makkaveev et al., 2017; Osadchiev et al., 2017). The surface water layer (0–10 metres) along the transect was freshened up to 25 psu with Yenisei water (Makkaveev et al., 2017). A strong vertical salinity gradient was observed in the layer at 10–20 metres. The bottom water salinity varied from 33.8 to 34.8 psu. The riverine waters most influenced the central part of the transect (from 76°58N to 78°35N) (Makkaveev et al., 2017). The high concentrations of minerals and total phosphorus, oxygen saturation below 75%, accumulation of organic matter and its active oxidation indicate an orographic depression. The dominance of minerals over organic forms of phosphorus and high concentration of silicon reveals the beginning of the nutrient recycling process in the southern part of the transect (Makkaveev et al., 2017).

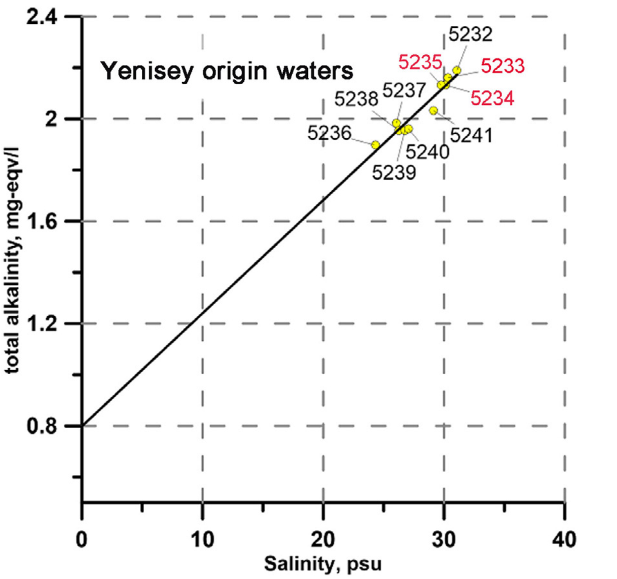

Fig. 2. Alk/S ratio in the surface layer of the cross-section showing freshwater input from the Yenisei River. Red indicates additional hydrochemical stations 5233, 5234 and 5235 without meiobenthos sampling.

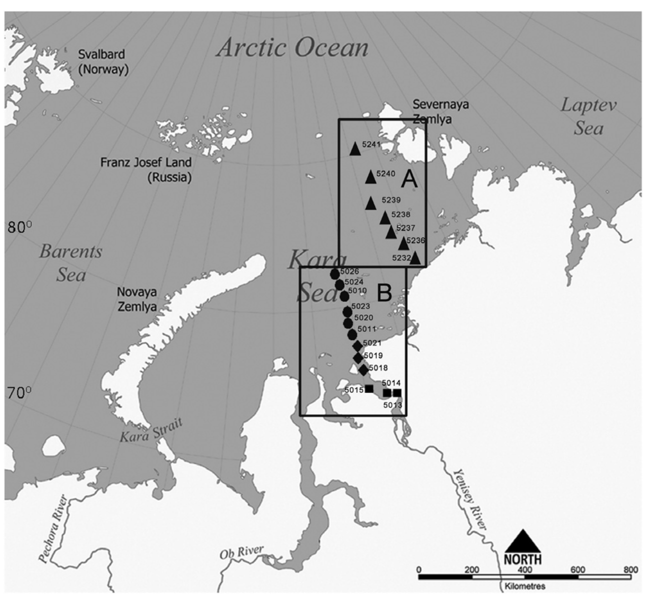

Fig. 3. Kara Sea map with two transects. Map showing the location of meiobenthos sampling stations visited in September 2011 (Portnova et al., 2017) and this study. Transect A — triangles, transect in the present study. Transect B (stations 5013–5026) the Yenisey Gulf and the adjacent part of the Kara Sea shelf: square — freshwater part of the Yenisei Gulf, diamond — estuary, circle — open central sea.

2.2. Study area compared with other data from the Kara Sea

Portnova et al. (2017) report that the meiofauna was studied at 12 stations in the Yenisei Gulf and adjacent Kara Sea shelf. The material was collected in September–October 2011. The stations were located in the open central sea, characterized by marine conditions and the estuary area (Yenisei Gulf) influenced by huge runoff from the Yenisei River (Fig. 3).

In the study area, the depth ranged from 9 to 62 m and the bottom salinity from 0.1 to 34.0 psu. The length of the transect was 550 km. In 2011, the largest part of the Kara Sea was influenced by the Yenisei River runoff, which became mixed with Arctic waters from the St. Anna Trough area. The river–seawater mixing zone during the cruise was characterized by a complicated structure and consisted of two parts – a vertical frontal zone passing between stations 5013 and 5015 and a horizontal frontal zone spanning the southern part of the sea up to station 5026 (Lein et al., 2013; Kravchishina et al., 2015; Makkaveev et al., 2015). The bottom sediment types were distributed from medium-grained sand with aged plant detritus at the freshwater part of the Yenisei Gulf through silt sediments at the estuary to mixed sand/silt and median-grain sands on the shelf. The transect had two main areas with mass sedimentation and oxidation of organic matter (stations 5015, 5020 and 5021) (Portnova et al., 2017).

2.3. Statistical analysis

We used the PAST software (Hammer et al., 2001) to describe differences in the spatial distribution of meiobenthos among the cores at each station and among the different stations. Similarities in meiobenthos compositions (data for the uppermost 5 cm of sediments from all stations) were analysed using a cluster analysis. We used two different similarity indices: Bray–Curtis and the Dice-Sørensen index (Gallagher, 1999).

Bray–Curtis measure for abundance data. The 'Bray–Curtis' is the similarity between two operational units j and k, each defined by a set of N attributes x_{ij} and x_{ik}:

$$\text{Bray–Curtis}_{\text{jk}} = \sum_{\text{i}=1}^{N} |x_{ij} - x_{ik}| / \sum_{\text{i}=1}^{N} (x_{ij} + x_{ik})$$

In this study, the units are the sampling stations from the transect, and the attributes are the meiobenthic taxa found at those stations. The Dice (Sørensen) coefficient was used for absence-presence (coded as 0 or positive numbers). Using 'M' for the number of matches and 'S' for the total number of taxa with a presence in just one column, we have

$$\text{Dice similarity} = 2M/(2M + S)$$

The differences in meiobenthic structure among the different samples were assessed by non-metric Multi-Dimensional Scaling (MDS), using the Dice similarity measure (Hammer et al., 2001) with log-transformed abundance data. Differences in the total densities of meiobenthos among the stations were checked with one-way ANOVA. The Tukey test compares the difference between each pair of means (of total density) with appropriate adjustments for multiple testing. Canonical Correspondence Analysis (Legendre and Legendre, 2012) is the correspondence analysis of a station/taxon matrix where each station has given values for one or more environmental variables (temperature, depth, grain size, oxygen, etc.). We used the following measures for the diversity (as realized in PAST): (1) number of taxa (S); total number of individuals (n); (2) dominance = 1 − Simpson index (Hammer et al., 2001). It ranges from 0 (all taxa are equally present) to 1 (one taxon completely dominates the community): $\text{D} = \sum (n_i/n)^2$, where n_i is number of individuals of taxon i. (3) Shannon index (Hammer et al., 2001), a diversity index, taking into account the number of individuals and the number of taxa. It varies from 0 for communities with only a single taxon to high values for communities with many taxa, each with few individuals: $\text{H} = -\sum (n_\text{i}/\text{n}) * \ln (n_\text{i}/\text{n})$. (4) Pielou index (Heip and Herman, 2001). The Shannon diversity divided by the logarithm of the number of taxa. This measures the evenness with which individuals are divided among the taxa present.

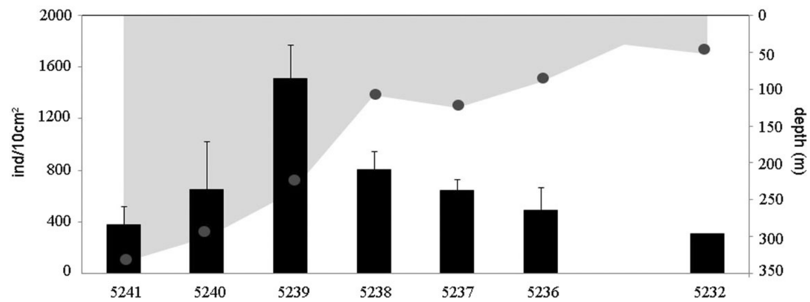

Fig. 4. Density (mean ± SE, ind./10 cm^2) of the total meiobenthos.

2.4. Sampling and treatment of meiofauna samples

All samples (depth range 52–325 m) were collected at the eastern part of the Kara Sea shelf and the southern edge of the Voronin Trough during the ARK 63 cruise of the RV *Mstislav Keldish* using a Neimistö corer (Niemistö, 1974). In seven out of ten stations, sediment samples were collected to study the meiobenthos; three additional stations (5233, 5234, and 5235) were chosen for analysing only hydrochemical characteristics (Table 1).

Concurrent with the sampling, environmental parameters such as the depth, surface and bottom salinity, bottom water temperature in the water column, nutrient (phosphates, silicates, nitrogen) concentrations, grain size and C_{org} were measured from the same Neimistö corer sediment sample (Lein et al., 2013; Makkaveev et al., 2017). Sediment samples for particle size determination and organic matter content were collected at the same stations as the meiofaunal samples. Grain-sizes of the upper 5 cm layer of sediments were measured by ANALYSETTE 22 MicroTec Plus laser diffraction (analyst I.N. Semenkov). The volume-weighted mean particle size, silt-clay content (volume percent of particles < 63 μm) and the Trask sorting coefficient So = (P25/P75) 0.5 were calculated where P25 and P75 were the 25th and 75th percentiles for particle size distribution (Eleftheriou, 2013). Organic carbon was measured by the dichromate oxidation (analyst A.A. Usacheva, IGEM RAS). Four cores per station were subsampled for meiobenthos using a 20 ml disposable syringe with a cut-off anterior end (inner diameter 2 cm). Samples were analysed down to a depth of 5 cm. Samples for meiobenthos were fixed in a 4% formaldehyde filtered saltwater solution. All meiobenthos samples were stained with Rose Bengal and washed through a sieve with a 40 μm mesh in the laboratory. The meiobenthos was extracted by centrifugation in Ludox (Heip et al., 1985). All organisms retained on a 40 μm sieve were counted and sorted into major taxa.

3. Results

3.1. Major taxa

A total of 10 major meiofaunal taxa, excluding copepod nauplii, were recorded in the eastern part of the Kara Sea (Table 2).

At the Kara Sea shelf and the slope of the Voronin Trough, 4–6 taxa were noted. Only at station 5239 were nine taxa registered. At all stations, nematodes, harpacticoid copepods and polychaetes were observed, whereas ostracods and bivalves had an occurrence frequency of 85%, and kinorhynchs, 70%. Other taxa occurred with a frequency of 14%. Tardigrades, halacarid mites and juvenile sipunculids were noted only at slope station 5239 (241 m). In contrast, isopods were noted only at the outer shelf at stations 5236 and 5237 (Table 2).

Meiofaunal abundances ranged from 302 ± 46 ind./10 cm^2 (the shallowest shelf station 5232) and 1510 ± 362 ind./10 cm^2 (station 5239) with the mean density (682 ± 403 ind./10 cm^2) for the eastern part of the Kara Sea. The average meiofaunal abundance at the shelf was 560 ± 214 ind./10 cm^2 (stations 5232, 5236, 5237, 5238), and at the slope, 846 ± 590 ind./10 cm^2 (stations 5239, 5240, 5241). The meiobenthos density and diversity increased from the shelf stations to the Voronin Trough slope and decreased again at the deepest station of the transect (Fig. 4).

However, a one-way ANOVA comparison of total density among the stations did not show any significant difference among the six stations ($p > 0.05$). A Tukey's comparison of total density revealed significant differences only between two stations, 5239 and 5232: the density at station 5239 was significantly higher than that at 5232 ($p < 0.001$).

The density of nematodes ranged from 143 ± 45 ind./10 cm^2 (inner shelf station 5232) to 1220 ± 226 ind./10 cm^2 (station 5239). The highest density of nematodes was observed at the station located on the slope, while the lowest value was at the shelf station. Nematodes represented from 63 to 91% of the total meiofaunal abundance. On average, nematodes amounted to 86% for the eastern part of the Kara Sea.

Harpacticoids were the second most important group in terms of meiofaunal abundance. The total harpacticoid abundance was relatively low, on average 42 ± 17 ind./10 cm^2. The highest density was found at station 5239 (76.3 ind./10 cm^2), and the lowest at station 5236 (19.8 ind./10 cm^2). The highest proportion of harpacticoid copepods in the meiobenthos was at the inner shelf station 5232 (19%) and at the deepest station 5241 (11%). Harpacticoid copepods constituted 4%–7% of the total abundance at all other stations. Polychaetes and ostracods were the next important groups in terms of abundance. The density of polychaetes ranged from 7 ind. (stations 5238, 5240) to 19 ind./10 cm^2 (stations 5232 and 5237).

The analysis based on environmental data (Fig. 5) showed that the first component accounted for 65% of the total variability and reflected the general trend along the transect from the shallower shelf with coarse sediment (station 5232, right lower corner) to deeper and silty sediments. The second and third components accounted for 17.7% and 10% of the total variance and correlated with the total organic carbon in the sediment and oxygen (stations 5238, 5239 *versus* all other stations).

Ostracods, harpacticoid copepods and polychaetes revealed positive correlations with shallow-water coarse fraction, C_{org}, Si and PO_4 values. Kinorhynchs preferred deep-sea silt sediments. Bivalves were the most dependent on oxygen among all the taxa (Fig. 6).

3.2. Comparisons with other data from the Kara Sea

The comparisons of the taxonomic composition and quantitative data of the meiobenthos obtained by us in this study with previous data indicated a high taxonomic similarity (70%) of the eastern part of the Kara Sea with the open central sea and estuarine mixing zone (Fig. 7).

Stations in the freshwater part of the Yenisei Gulf (stations 5013, 5014, and 5015) are very different both from each other

Table 1
List of sampling stations, locations, sampling dates, depths, and variables characterizing the near-bottom water and sediments (0–5 cm) (S — salinity, Temp — temperature, O_2 — percentage of oxygen, C_{org} — total C org, Sorting — Trask sorting coefficient, Silt — % silt content, Si — silicate concentration, NO_3 — nitrogen, PO_4 — phosphate concentration). Meiobenthos stations are shown in bold.

Station	Data	Latitude	Longitude	Depth (m)	S (psu)	Near bottom water					Sediment		
						Temp. (°C)	O_2 (%)	Si μM	NO_3 μM	PO_4 μM	C_{org}%	Sorting	Silt
5232	19.09.2015	75°53, 3′	089°30, 5′	52	33.8	−1.03	75.2	11.84	8.36	0.81	1.32	213.6	55
5233	19.09.2015	76°08, 7	089°21, 1	48	33.9	−1.04	71.1	10.99	8.00	0.69	–	–	–
5234	19.09.2015	76°33, 2	088°82, 3	45	33.9	−1.04	74.5	9.38	7.72	0.61	–	–	–
5235	19.09.2015	76°58, 3	088°43, 3	35	33.9	−1.02	76.4	6.62	7.31	0.52	–	–	–
5236	19.09.2015	76°58, 1′	087°50, 4′	90	33.9	−1.05	72.3	7.67	6.71	0.96	0.85	73.33	67
5237	20.09.2015	77°30, 0′	087°13, 2′	125	34.2	−0.91	78.6	7.77	9.63	0.44	1.25	34.54	84
5238	20.09.2015	78°00, 9′	087°37, 3′	108	34.6	−0.43	86.0	3.91	6.54	0.44	0.58	70.64	58
5239	21.09.2015	78°35, 9′	088°03, 8′	241	34.7	−1.37	89	4.76	8.77	0.47	0.75	84.51	62
5240	21.09.2015	79°16, 0′	087°37, 8′	301	34.8	−1.42	88	6.57	9.44	0.59	1.61	57.01	75
5241	21.09.2015	80°00, 0′	085°32, 0′	335	34.8	−0.9	85.4	3.91	10.42	0.66	1.52	31.87	89

Table 2
The average density (mean ± SE, ind./10 cm^2) of each meiobenthic group and of the total meiobenthos, in the 0 to 5 cm sediment layer. Nauplii were counted in the total meiobenthos density but did not count as a taxon. S – number of taxa.

Station	5232	5236	5237	5238	5239	5240	5241
Depth (m)	52	90	125	108	241	301	335
Nematoda	143 ± 45	419 ± 170	558 ± 38	662 ± 125	1220 ± 226	553 ± 338	312 ± 139
Harpacticoida	45 ± 3	20 ± 11	33 ± 7	31 ± 3	76 ± 18	46 ± 21	43 ± 9
Tardigrada	0	0	0	0	1	0	0
Kinorhyncha	0	0	5 ± 2	2	1	1	1
Ostracoda	14 ± 4	3	0	1	10 ± 6	9 ± 5	2
Polychaeta	19	16 ± 10	19 ± 13	7 ± 4	18 ± 9	10 ± 8	6 ± 3
Bivalvia juv	0	1	5 ± 2	1	14 ± 5	1	5 ± 2
Isopoda	0	5 ± 3	3	0	0	0	0
Halacarid mites (Acari)	0	0	0	0	2	0	0
Sipunculida juv	0	0	0	0	1	0	0
Nauplii	81 ± 5	25 ± 11	22 ± 18	99 ± 40	169 ± 60	34 ± 12	10 ± 5
S	4	6	5	6	9	6	6
Total meiobenthos	302 ± 46	489 ± 124	645 ± 166	804 ± 198	1510 ± 362	650 ± 164	378 ± 93

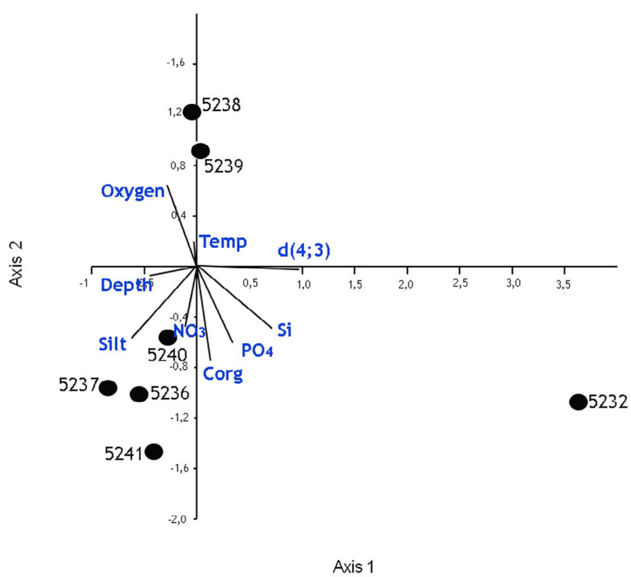

Fig. 5. Canonical correspondence analysis based on the environmental factors. A plot of stations versus environmental variables is shown. The environmental variables are depth (Depth), Temp (temperature), O_2 – percentage of oxygen, C_{org} – total C_{org}, d (4;3) – mean particle size, Silt – silt content, Si – silicate concentration, NO_3 – nitrogen, PO_4 – phosphate concentration.

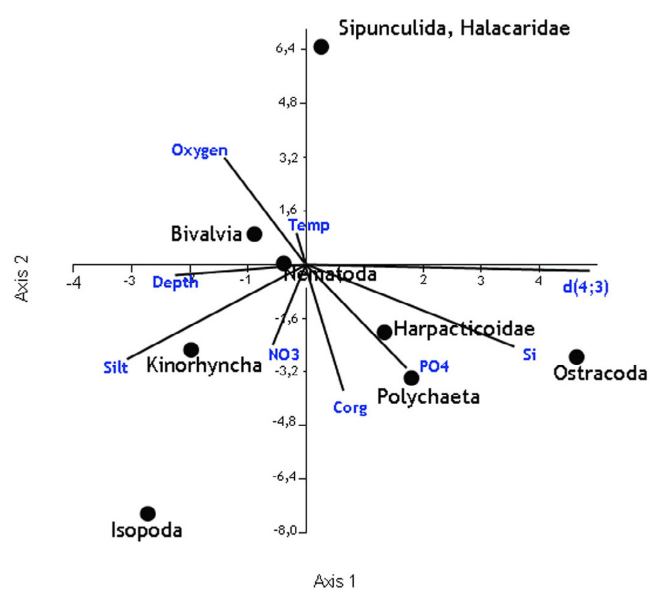

Fig. 6. Canonical correspondence analysis based on square-root transformed meiobenthos abundance. The environmental variables are Depth — depth, Tem — temperature, O_2 — percentage of oxygen, C_{org} — total C org, d (4;3) — mean particle size, Silt — silt content, Si — silicate concentration, NO_3 — nitrogen, PO_4 — phosphate concentration.

and from all other stations in terms of meiofauna composition. The meiobenthos of this part of the transect was the least diverse; only nematodes were present at all stations (Table 3), while the meiofauna was more diverse at the shelf and in the estuarine mixing zone (stations 5018, 5019, 5021).

The taxonomic structure of the meiobenthos at the eastern part of the Kara Sea was closer to the central part of the shelf (Fig. 7). The abundance of the meiobenthos at the eastern part of the Kara Sea (all stations except 5239) is comparable to that in the freshwater parts of the Yenisei Gulf (stations 5013 and 5015) and at the central

Table 3
The characteristics of the taxonomic diversity of the meiobenthos at stations in the eastern part of the Kara Sea, Yenisei Gulf and adjacent parts of the Kara Sea shelf. S – number of taxa.

Location	Freshwater zone of the Yenisei Gulf			Estuarine mixing zone			Open central sea					Voronin Trough transect						
Stations	5013	5014	5015	5018	5019	5021	5011	5023	5010	5024	5026	5232	5236	5237	5238	5239	5240	5241
S	5	2	2	5	7	7	6	8	8	9	9	5	7	6	7	10	7	7
Dominance (D)	0.521	0.739	0.579	0.803	0.631	0.682	0.637	0.909	0.664	0.880	0.779	0.459	0.815	0.806	0.884	0.829	0.804	0.783
Shannon	0.842	0.429	0.611	0.403	0.762	0.633	0.783	0.256	0.787	0.340	0.490	1.049	0.453	0.464	0.287	0.420	0.445	0.558
Pielou index	0.523	0.619	0.882	0.250	0.392	0.325	0.437	0.123	0.379	0.155	0.223	0.652	0.233	0.259	0.147	0.182	0.229	0.287

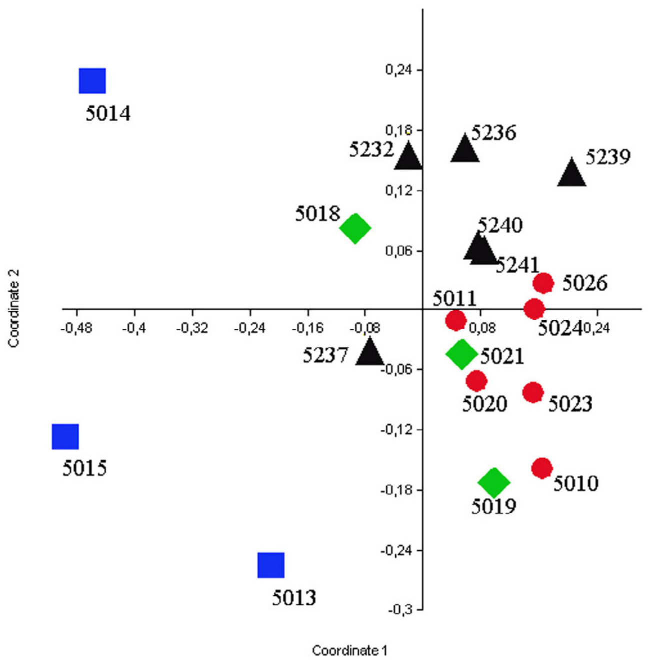

Fig. 7. MDS ordination of stations based on similarity in taxonomic composition quantified with Dice (Stress = 0.07). Black — transect in the present study, blue — freshwater part of the Yenisei Gulf, green — estuarine mixing zone, red — open central sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

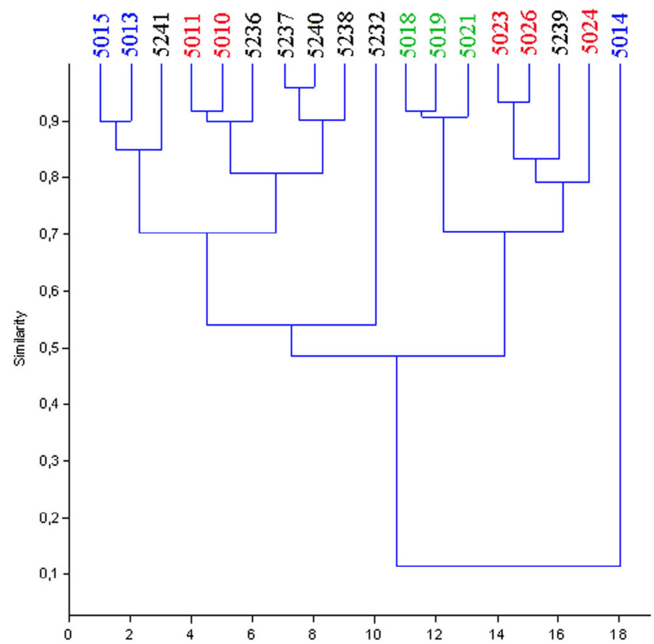

Fig. 8. Dendrogram of the total meiobenthos at all sites using complete linkage clustering from Bray–Curtis similarities. Communities were separated into two clusters. One cluster combines Voronin Trough transect stations with stations enriched with organic carbon from the central part of the Kara Sea shelf. The second cluster combines stations from the Yenisey Gulf estuary and central part of the shelf. Black — Voronin Trough transect; blue — freshwater part of the Yenisei Gulf, green — estuarine mixing zone, red — open central sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

part of the shelf stations enriched with organic carbon (stations 5010 and 5011). Station 5239 was closer to stations 5023, 5024, and 5026 at depths of 23–62 m (Fig. 8) in terms of meiofaunal abundance.

4. Discussion

The composition and quantitative distribution of the meiobenthos in the Kara Sea were studied along the eastern coast of the Novaya Zemlya archipelago from Abrosimov Bay to Stepovoi Bay, in the Novozemelskaya Depression, along the western coast of the Taimyr Peninsula and in the Yenisei Gulf (Pogrebov et al., 1997; Galtsova et al., 2004; Alexeev and Galtsova, 2012). The analysis of the meiobenthos' taxonomic composition on the Arctic shelf showed 9 taxa of the temporary meiobenthos (the larvae of macrobenthos) and 12 taxa of the permanent meiofauna (Alexeev and Galtsova, 2012). Nine major taxa were identified in the present study that confirms the relatively high richness of the meiobenthos at the Kara Sea shelf.

The meiobenthic density (682 ± 403 ind./10 cm^2 on average) was similar to the corresponding densities in the central Arctic Ocean and Arctic shelf seas (Vanaverbeke et al., 1997; Soltwedel, 2000; Vanreusel et al., 2000; Miljutin et al., 2012). However, the abundance of the meiobenthos from the eastern part of the Kara Sea was lower than in the open central part and in the Yenisei Gulf. The general distributions of water hydrochemical data, chlorophyll and nitrates at the Voronin Trough transect correspond better to the period of transition from summer to autumn. The rates of photosynthesis were low and the biological activity was declining (Makkaveev et al., 2017). The low oxygen saturation of the water combined with the high content of ammonium nitrogen indicated the predominance of degradation processes of organic matter and the absence of the active phase of photosynthesis. The oxidation processes of organic matter in the water column reduced the food flow for the meiobenthos. Silty sediments with high values of C_{org} negatively correlated with the meiofaunal density. Stations 5010, 5011, 5013, and 5014, combined by the Bray–Curtis similarity with the Voronin Trough transect stations, were characterized by coarse sediment, low levels of near-bottom dissolved oxygen and dissolved organic matter (Sukhanova et al., 2015; Portnova et al., 2017).

A previous study in the Kara Sea reported that the low abundance of meiobenthos in the Novaya Zemlya bays and in the Novozemelskaya Depression was associated with the reaction of the meiobenthos to radioactive contamination (Barescut et al., 2009). The discordance between the differences in meiobenthic abundance may probably also be explained by the sieve mesh size used in the earlier studies. In the present study, meiofaunal samples were washed through a sieve mesh size of 40 μm and extracted by means of centrifugation with Ludox, while in the earlier studies meiobenthic samples were washed through a sieve with mesh size 63 μm and counted (Kulakov et al., 2004). Using the sieves for meiobenthos sorting with larger mesh sizes than used in modern studies is typical of Galtsova's studies (Galtsova and Sheremetevsky, 1985; Galtsova et al., 2004). Miljutin et al. (2012) noted that the meiobenthic density in the Kandalaksha Depression at a depth of 270 m is much higher than in Galtsova (1991) and may be explained by the extraction technique used a sieve with a mesh of 32 μm, in contrast to Galtsova's sieve mesh size of 90 μm. As demonstrated in Leduc et al. (2010), using a 63 μm mesh sieve has a substantial effect on nematode abundance estimates. Nematodes account for 80%–90% of the abundance of all metazoans and are among the most diverse and widespread organisms in benthic habitats (Vanreusel et al., 2010; Semprucci and Balsamo, 2012). The data for 1250 m suggest that the 63 μm mesh sieve retains approximately 50%–80% of the deep-sea nematode abundance, while the 45 μm mesh sieve retained 79%–90% of the nematodes in the samples (Leduc et al., 2010). Nematode relative abundance increases with depth and usually reaches 70%–95% at 24–400 m depth in polar and temperate regions (Vanaverbeke et al., 1997; Soltwedel, 2000; Kotwicki et al., 2004; Vanreusel et al., 2010; Miljutin et al., 2012). Our results are in agreement with these findings, with nematodes representing approximately 86% of the meiobenthic metazoans in the eastern part of the Kara Sea.

Harpacticoid copepods were the second most abundant group. In the Yenisei Gulf and the adjacent parts of the Kara Sea, the total harpacticoid copepod abundance was 64.4 ind./10 cm^2 (Garlitska and Azovsky, 2016). On the Russian Arctic shelf, the abundance of harpacticoids varied from 3 to 970 ind./10 cm^2 (Alexeev and Galtsova, 2012), and in the White Sea at a depth of 270 m, the density was 65.1 ± 21.4 ind./10 cm^2 (Miljutin et al., 2012). In the outer basin of the Kongsfjorden, Spitsbergen, the mean abundance was 32.7 ind./10 cm^2; in the Laptev Sea at the depth of 38 m it was 140 ind./10 cm^2, and 52.5 ± 15.2 ind./10 cm^2 at the depth 24–85 m in the southeastern Beaufort Sea (Kotwicki et al., 2004; Bessière et al., 2007). Thus, the relative abundance of harpacticoids recorded in the eastern part of the Kara Sea during this study (from 4 to 19% of meiobenthic metazoans) was at the lower limit of reported values (42.2 ± 17.7 ind./10 cm^2), and their relative density can be considered fairly low. However, at station 5239 (241 m), the number of harpacticoids doubled (76.37 ind./10 cm^2). Other groups were scarce. This was again in agreement with the majority of studies on meiobenthos from the subtidal zone, the continental slope and the abyss (Soltwedel, 2000; Kotwicki et al., 2004; Bessière et al., 2007; Miljutin et al., 2012).

The southernmost station of the transect differs with its low meiobenthic density and diversity. Station 5232 is located in the orographic depression with an accumulation of organic matter and intense oxidation in the sediment. Organic carbon, being directly related to food supply, is one of the major environmental parameters influencing the distribution of the meiobenthos (Rex et al., 2006). Generally, the most common response of meiobenthos to organic enrichment is a significant decrease in total abundance due to changes in the sedimentary characteristics (i.e., reduced oxygen fluxes at the water-sediment interface). High primary productivity in the near-shore waters promotes high biomass but low species richness (Azovsky et al., 2012). According to our results, ostracods and harpacticoid copepods revealed positive correlations with high C_{org} values and the coarse sediment fraction. Some authors recorded significant increases in the abundance of harpacticoid copepods and ostracods with increased levels of organic matter (sum. Azovsky et al., 2012; Mesquita-Joanes et al., 2012). Several experimental studies have demonstrated the high tolerance of some ostracod species to hypoxia (Jahn et al., 1996; Rossi et al., 2002; Frontalini et al., 2018). Corbari et al. (2004, 2005) suggested that ostracods actively search to find low oxygen concentrations in the sediment that match their tissues' low O_2 partial pressure, as an ancient strategy to cope with environmental changes in O_2 concentration and to keep the internal pressure close to the original early conditions of ostracod evolution. The structure of the harpacticoid species assemblages was often determined by the type of sediments (Hicks and Coull, 1983). Some authors have reported higher densities and diversities of harpacticoid copepods in sandy than in silty sediments (Rybnikov et al., 2003; Garlitska and Azovsky, 2016), but others have suggested the opposite trend (Chertoprud et al., 2010). The effect of sediment type on harpacticoid copepods could be attributed to the higher physical heterogeneity of sites with mixed sediments (sand/mud sediments) compared to silts or muds (Azovsky et al., 2012; Chertoprud et al., 2017).

A high meiobenthic abundance, comparable to the central part of the Kara shelf and estuary, was only found at station 5239 (241 m depth). Tardigrades, halacarid mites, and juvenile sipunculids appeared at station 5239, while the abundance of nematodes, harpacticoid copepods with nauplii and juvenile bivalves reached a maximum. Anisimova et al. (2003) showed a high diversity and abundance of macrobenthos in the Voronin Trough at 241 m depth. These authors related the peak of biodiversity with the high concentration of organic matter arriving with the intermediate Atlantic waters. The Atlantic intermediate water masses were observed in the Voronin Trough between 180 and 250 m depth (Anisimova et al., 2003). The intermediate Atlantic waters were marked by positive temperature and oceanic salinity and were below the Arctic waters of local origin in the area considered (Dmitrienko et al., 2010). The warm and salty Atlantic waters play a special role in the thermal balance of the Arctic Ocean and enter the Arctic Ocean by two major inflows through the Fram Strait and the Barents Sea shelf, merging just north of the Kara Sea area (Dmitrienko et al., 2010).

According to our data, with increased distance from the coastline, the values of organic matter decrease and the sediments become silty and more oxygen enriched. The importance of depth, productivity and sediment composition to the meiofauna is well documented (Vanaverbeke et al., 1997; Giere, 2009). It is reasonable to suppose that the high meiobenthic abundance and diversity at station 5239 is provided by high organic matter fluxes at the boundary of the water masses, increasing the oxygen and silt fraction in the sediment.

Piepenburg and Schmid (1997) showed that the abundances and compositions of the Arctic benthos are largely influenced by mesoscale pelagic processes, thereby highlighting pelagic-benthic coupling in high-latitude seas. Previously, an indirect relationship was shown between the hydrodynamics, concentrations of suspended matter, sedimentation processes and the trophic structure of the benthos in the Kara Sea (Jørgensen et al., 1999; Kozlovskiy et al., 2011; Vedenin et al., 2015). Our case study in the Voronin Trough demonstrates the result of the complex influence of all factors acting jointly.

5. Conclusions

In this study, we showed that the distribution and diversity of the meiobenthos are affected by the depth, types of sediments, organic matter content, hydrology and hydrochemistry in the eastern part of the Kara Sea basin and southern edge of the Voronin Trough. The meiobenthos composition was similar between the Yenisei River estuary and the central and eastern parts of the shelf despite the variety of physiographic conditions in the Kara Sea. The abundance of meiofauna in the eastern part of the Kara Sea shelf was lower than in the central part and the Yenisey River estuary. The orographic depression, accumulation of organic matter and its active oxidation in the sediment have a negative impact on the meiobenthos diversity.

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