Siberian river run-off in the Kara Sea
R. Stein, K. Fahl, D.K. Fütterer, E.M. Galimov and O.V. Stepanets (Editors)

Benthic fauna of the southern Kara Sea

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Abstract

The ecosystem of the Kara Sea is subjected to strong Arctic as well as continental influences (river runoff) and, together with its coastal region, expected to become increasingly used for navigation and exploitation (e.g. of oil and gas resources) and changed by global climate alterations. The benthic compartment of the system is insufficiently known. Therefore, quantitative samples of the benthic invertebrate fauna were collected for analyses of species composition, distribution and biogeographic and community structures at 35 stations at water depths between 17 and 200 m from the estuarine and the southern parts of the Kara Sea in 1993. A total of 500 zoobenthos taxa were identified. Shannon diversity indexes varied from 0.42 to 5.35. The lower values correspond to estuarine parts of the study area, where other characteristics of the bottom fauna also reflect the strong influence of fresh water outflow from the Ob and Yenisei. Abundance varied from 750 to 17000 ind. m^{-2} and gross wet weight biomass from 40 to 650 g m^{-2} from estuarine areas toward the open sea. In general the high biomass values in the offshore area (from 170 to 650 g m^{-2} or 9-21 g C_{org} m^{-2}) are not consistent with the view that the Kara Sea is oligotrophic. Comparison of the community structures determined by the "relative production method" with previous investigations exhibits similar general trends despite the differences in methodological approaches and the interval of 50 years between observations. Similarities were found mainly in the southern, stressed part of the study area, while dominant species were different in its northern part.

1 Introduction

The bottom fauna of the Kara Sea was studied since the end of the 19th century. However, the first observations provided faunistic information only sporadically. In contrast, studies carried out in the 1920-40s were quite regular, and these data were used for descriptions of species composition, biogeographic structure and quantitative patterns (Gorbunov, 1934, 1937; Gurjanova, 1933, 1935; Pergament, 1945; Filatova ,1957; Filatova and Zenkevich, 1957; Kusnetsov, 1980) and serve as basis of our current knowledge about the bottom fauna of the Kara Sea. The most comprehensive paper (Filatova and Zenkevich, 1957) on the quantitative distribution and biocenotic structure was based on data sampled at 35 stations in 1927, 1935 and 1945. Obviously such data can not be easily compared and taken as quasi-synoptic. In 1975, PINRO (Polar Institute of Fisheries Research and Oceanography) carried out a benthic survey in the western Kara Sea. However, samples were not identified in detail,

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and reliable information has been obtained only for biomass distribution of zoobenthos in the south-western region (Antipova and Semenov, 1989). Later, in 1990-1991, few expeditions took benthic samples in the Baydara Bay for impact assessments of a construction of a gas pipe-line, providing new data about the zoobenthos in the inner part of the Bay (Denisenko et al., 1993; Kucheruk et al., 1998).

Information is relatively sparse for the estuarine inner part of the Ob Bay (Leschinskaya, 1962; Kusikova; 1984; Cochrane et al., 1997, Khlebovich, Komendantov, 1997; Sirenko, 1998, Jørgensen et al., 1999). However, any quantitative information was absent for the coastal shelf area immediately outside the mouths of Ob and Yenisei Bays as well as for the estuarine area of the Yenisei Bay till the 1990s (Jørgensen et al. 1999). The whole known data are very scattered, and such information as published by Kiyko and Pogrebov (1997) and based on completely different methods of sampling is too general. Studies made within the new Russian-German cooperative project "SIRRO" are still in an early stage of evaluation (Deubel et al., this volume).

The aim of the present work is to further the understanding of the bottom fauna structure of the Kara Sea ecosystem including its south-western part. Such baseline studies will enable to identify future changes in species composition and benthic biocenoses and to relate changes to possible effects of human or natural impacts. As the Kara Sea has a transitional position between the Barents Sea, strongly influenced by Atlantic waters, and the more continentally affected Laptev and East Siberian Seas, climatic changes may also be identified by shifts in the distribution and composition of the Kara Sea bottom fauna.

The benthic fauna was studied during surveys with R/V "Dalniye Zelentsy" of the Murmansk Marine Biological Institute RAS in August/September 1993 (Jørgensen et al, 1999) and with R/V "Dmitriy Mendeleev" during an expedition of the P.P. Shirshov Institute of Oceanology in the same year (samples were taken by S. Kühne, AWI Bremerhaven). Accordingly, our study is focused on the shallow coastal and shelf areas of the Kara Sea including the estuarine zones of Ob and Yenisei Bays. The sampling areas partly corresponded with zoobenthos stations carried out on board R/V "Akademik Boris Petrov" in 1997 (Poltermann et al., 1999; Deubel et al., this volume).

1.1 Study area

The investigations covered the shelf zone of the Kara Sea (Fig.1). Its main investigated part in the East lies under the strong influences of the runoff of Ob and Yenisei Rivers, while the Baydara Bay area in the West has a completely different oceanographic regime. Nevertheless, river outflow has some influence also on the circulation in the Baydara Bay. The river run-off shows a strong seasonal variability. The maximum discharge is observed in June after ice and snow melting (Matthiessen et al., 1999); annual amounts are 429 km^3 for the Ob and 620 km^3 for the Yenisei (Gordeev et al., 1995). The eastern study area comprises the "marginal filter" zone, where substantial parts of the suspended and dissolved loads of the rivers are deposited (Lisitzin, 1995). Freshened water spreads in the surface layer towards the continental slope by the Yamal Current.

The sea water in the zone of compensative inshore-directed currents near the bottom in front of the estuaries has temperatures between -1 and -2° C throughout the whole season. The surface temperature of the run-off may be higher and reach 10-15° C in summer time. The bottom temperature in the outer estuarine zone is below -1 C° while it increases towards the inner parts of the bays, where water temperatures vary strongly: The amplitude of the bottom water exceeds 5° C in inner, but only 0,5-1,0° in the outer parts of the estuaries

(Burenkov and Vasilkov, 1994). Under the river discharge, near bottom salinities vary from 5 to 6 in the mouths of the Ob and Yenisei bays during the seasons (Pavlov et al., 1996).

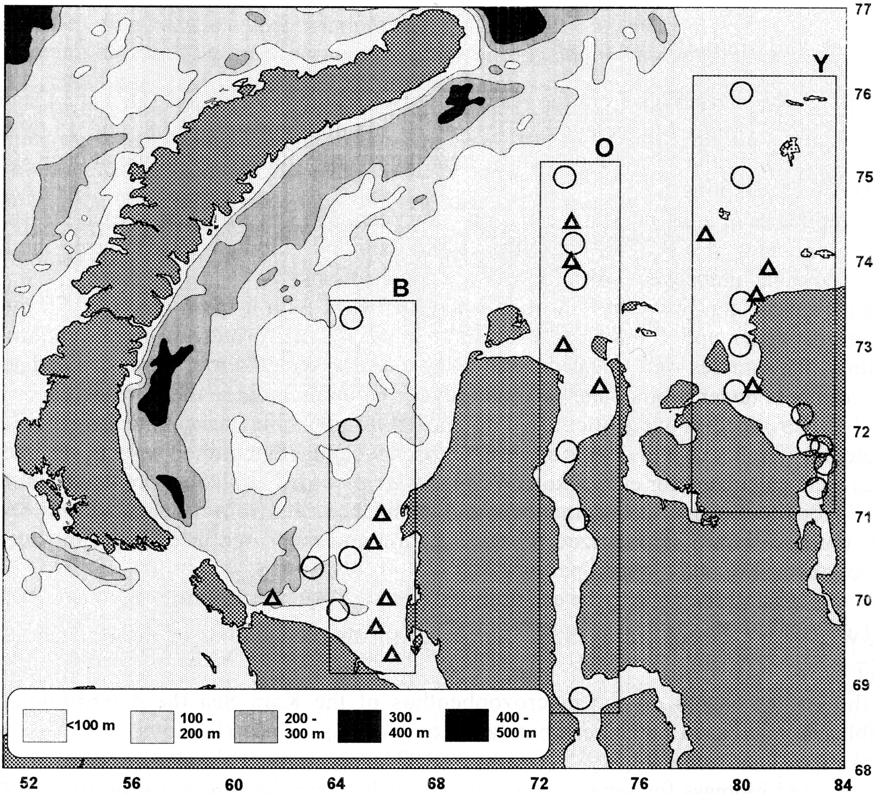

Fig. 1: Locations of stations in the Kara Sea.
Triangles - R/V "Dalniye Zelentsy", circles - R/V "D. Mendeleev" cruises in 1993.
B - Baydara Bay section, O - Ob section, Y – Yenisei section.

The water masses in the Baydara Bay and the western part of the study area are mainly influenced by inflow of transformed Atlantic water from the Barents Sea through the straits Yugorsky Shar and Kara Gate. Accordingly, this bay is characterised by oceanic salinity of 33 and negative temperatures between -1 and -2° C in winter time (Churun and Timokhov, 1998). In the summer period, temperature in the inner part of the bay is positive; but, the bottom water layer in the adjacent open sea has always negative temperatures (about -1° C) (Burenkov and Vasilkov, 1994).

An ice cover is present in the study area from late September to late May or even early June (Pavlov and Pfirman, 1994). However, during long actions of the wind in one direction, polynyas appear behind the fast ice. There are three polynyas in the Kara Sea: Ob-Yenisei, Yamal and Novaya Zemlya polynyas. The probability of appearance of the polynyas near the

Ob –Yenisei area is 50-70% in winter time and 30-50% in spring; near the Yamal Penisula 35-50% and near Novaya Zemlya 15-30% over the whole year (Atlas of the Oceans, 1980; Romankevich and Vetrov, 2001)

2 Material and Methods

Sampling was carried out from the research vessel "Dalniye Zelentsy" (DZ) at 14 stations and from R/V "Dmitri Mendeleyev" (DM) at 20 stations between 15.08. and 15.09.1993 (Fig.1, Table 1). Temperature and salinity were measured with a CTD-probe at each station before benthos sampling.

Five replicates of a 0.1 m^2 van Veen grab (van Veen, 1933) were taken at each DZ-station and two replicates of a 0.25 m^2 Ocean grab (Lisitzin and Udintsev 1955) during the DM-cruise. Additional grabs were taken for sediment descriptions.

Samples were gently washed through a bag of nylon with a mesh size of 0.75 mm in running sea water and fixed in 4% formalin neutralised by natrium-tetraborat. In the laboratory, the samples were washed again using a screen with 0.5 mm mesh size and sorted from sediments under a binocular to phyla level; the animals were then preserved in 70% ethanol. Later, species were identified to the lowest feasible taxonomic level. In each replicate, the number of individuals and summarised weights (determined with an accuracy of 0.1 mg) were calculated for each taxon. Weights were recorded as alcohol preserved total wet mass of blotted animals. Species numbers and abundance data from the two 0.25 m^2 or five 0,1 m^2 replicates were summarized for each station and then used to estimate the average values of abundance and biomass per m^2 .

Wet weight values (W_w) were converted to C_{org} using the equation $C_{org} = 0.0373 W_w^{0.98445}$, calculated by S.G. Denisenko for the zoobenthos of the Barents Sea in general.

In the earlier papers on the macrozoobenthos of the Kara Sea the determination of assemblages was based on either abundance or biomass values (Filatova and Zenkevich, 1957; Antipova and Semenov, 1989; Kusikova, 1974; Jørgensen et al., 1999). The use of both abundance and biomass for separating communities has been shown useful by Brey (1990), and suitable also for material collected from the Russian Arctic (Denisenko and Denisenko, 1990; Kucheruk et al., 1998). In our study, the following equation was applied to approximate the “relative production P_s “ of each species:

$$P_s = B_s^{0.75} * N_s^{0.25}$$

where B_s = biomass (g wet wt m^{-2}), and N_s = abundance (ind m^{-2}) of species “s”. This equation is rough, but sufficiently accurate and practical for the determination of communities.

For between-station similarity the Czekanowski-Soerensen index Cz was applied (Czekanowski, 1909; Soerensen, 1948), which is similar to the Bray-Curtis index (Bray and Curtis, 1957) and was adapted for quantitative data (Pesenko, 1982). The relative production value of each taxon was used in the calculations as follows:

$$Cz = 2 * \Sigma [\min (P_{sa}, P_{sb})] / \Sigma [(P_{sa} + P_{sb})]$$

where P_{sa} and P_{sb} = relative production of the species “s” at stations “a” and “b”, respectively.

Zoobenthic communities were identified by a standard hierarchical clustering of the stations using the Average Linkage Method of the "BioDiversity Pro" software (The Natural History Museum and The Scottish Association for Marine Science, 1997). The average similarity was calculated for the whole matrix to determine the level at which the samples should be assigned to separate communities.

The importance of a species is expressed by introducing the term "Species Validity Index" (SVI), calculated as the product of the frequency of occurrence and the mean relative production P_s of a species. The Shannon diversity index (H) was calculated on the basis of abundance values, using logarithms with the base 2. Homogeneity of communities (U, level of homogeneity) is taken here as an other term for evenness (H/H_{max}). Biogeographic terminology combines indications of the geographic zones of a species' origin (Atlantic, Pacific, Arctic), its biogeographic distribution (Boreal, Arctic, Boreo-Arctic) and the latitudinal zones of its occurrence (wide-spread, high Boreal etc.) (Ekman, 1957; Golikov, 1982).

3 Results

3.1 Environmental data

Baydara section

Most stations were located in the shallow inner Baydara Bay at depths from 20 to 45 m. In the open sea sampling was carried out at depth greater than 100 m. The hydrological regime at the stations correlated with depth. It was characterised by positive temperatures of the bottom water layer in the shallow coastal part. However, temperatures did not exceed 1°C. The bottom layer temperatures at deeper stations, even near the coast ranged from -1 to -1.5° C. Bottom salinity did not change considerably between stations and was near normal oceanic salinity (Fig. 2). Sediments in the inner parts of the Baydara Bay and near the Yamal Peninsula coast were characterised as sandy mud. Near the Vaygach Island and in the inshore and offshore parts of the section sediments were silty and very soft.

Ob section

The bottom profile along this section had only small changes of depths with low differences between neighbouring stations (Fig. 2). In the middle part of the Bay, opposite the Tas Bay, fresh water was found (Fig. 2); in the northern Bay, typical estuarine salinity (10-29) occurred, while the mouth area and the open sea were characterised by marine conditions. The changes in the hydrological regime were gradual, because there is no sill separating the bay from the sea. Accordingly, boundaries of the estuarine zone are not very pronounced in the Ob Bay (Golikov et al., 1990).

The bottom water of the marine part of the section was characterised by stable negative temperature at each station (-1.5°C) and by marine salinities (32-34). Sediments in the Ob Bay were mixed sandy muds with large portions of mud. Outside the Bay, soft mud with clay prevailed.

Yenisei section

The bottom profile is quite rugged along the Yenisei section, especially in the Yenisei Bay. There is a small depression in the central bay behind a shallow sill (Fig. 2).

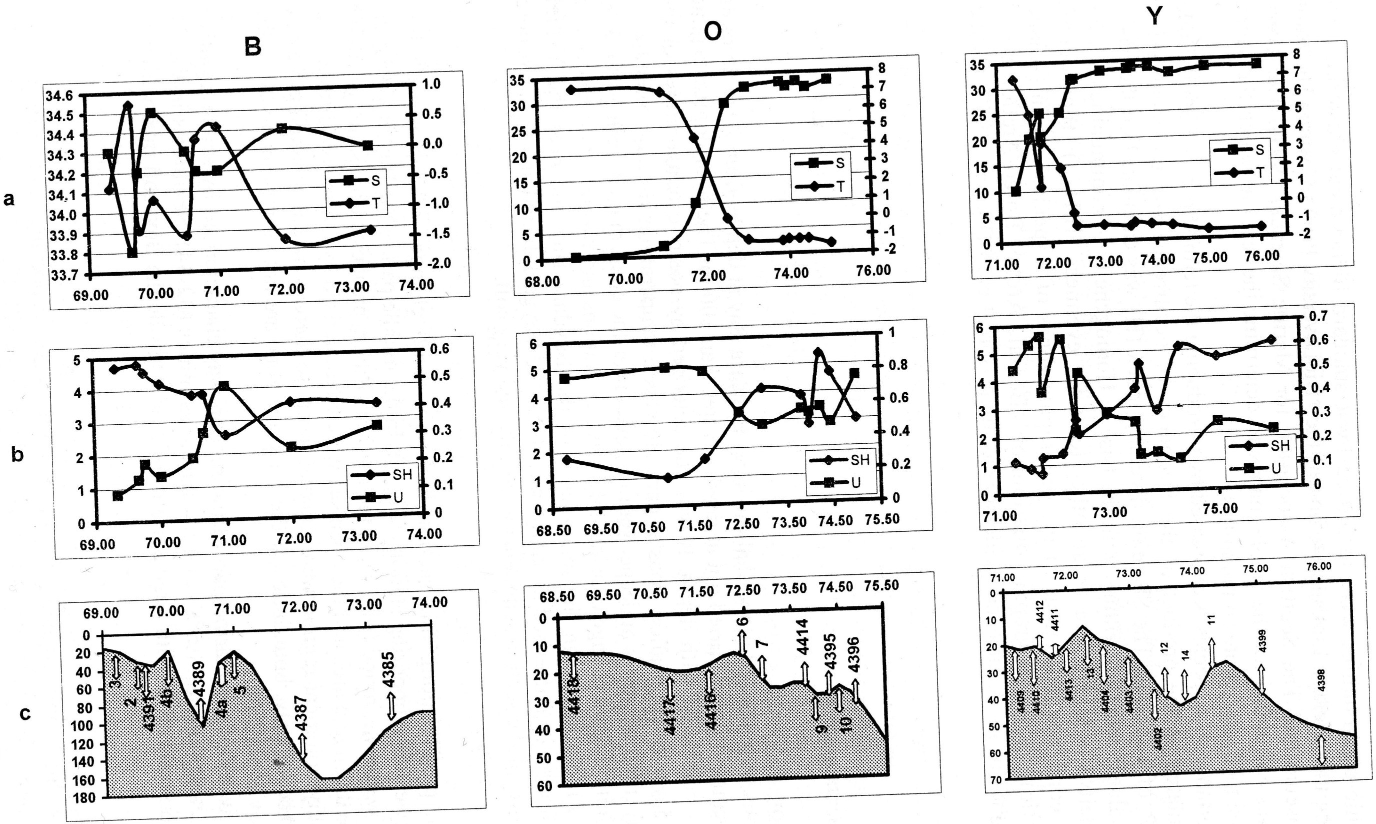

Fig. 2: Salinities and bottom temperatures (a), diversities (b) and bottom relief (c) at the stations along the sections in the Kara Sea.

These features have considerable influences on the water circulation in the bay and cause specific local patterns of the hydrological regime.

At the stations of the sill and in the depression, temperature and salinity change strongly with periodic inflows of cold marine waters with wind induced currents. In contrast to the other areas of the bay, temperature was negative. Water temperature increased up to 7° C, and salinity decreased to 10 in the inner part of the Bay. Thanks to the bottom relief and the backward current of marine water in the open part of the Bay north of the sill, river discharge was not reflected so strongly near the bottom there. Like along all sections the bottom sediments consist mainly of silt to clay or of sandy mud (see also Gorshkova, 1967).

3.2 Benthic fauna

Approximately 500 macro-zoobenthos taxa were determined from 13 phyla; 382 were identified to species level (full lists are available from the first author).

Baydara section

The total taxa number is 319 (223 identified species); included are animals inhabiting stations near the western coast of the Baydara Bay and opposite Yugorskiy Shar (St. 1). The highest species number (137) was found at St.1 on soft clayey sediment. Polychaetes dominated in species richness (43% of total species number), density and biomass (45% of total biomass). The dominant polychaetes (in biomass) were the deposit-feeding species *Spiochaetopterus typicus* and *Maldane sarsi*.

In the southernmost part of the section species numbers varied from 28 to 62. The fauna was more diverse at the shallow coastal sandy-mud stations (2, 3, 4a, 5) with water warming during summer time. Numbers of species decreased northward with increasing depths and decreasing temperatures (St. 4b, 4389, 4387, 4385). Polychaetes, molluscs and crustaceans predominated in species number at all stations and had the same decreasing tendency with depths as the fauna in total (Fig. 3a).

Relations of biogeographic groups varied, with Boreo-Arctic species dominating at all stations (77%) (Fig. 3b). The share of Arctic species was above 17%, much higher than the summarised Boreal taxa figures (3%). The occurrence of the Boreal forms was seemingly determined by the intensity of Atlantic water penetrating into the south-western part of the Kara Sea from the Barents Sea. At the inshore stations, their numbers reached 6, whereas only 1 or 2 species were found offshore or were absent there at all (St. 4389, 4387).

Regarding abundance, a relatively high share belonged to crustaceans, especially *Diastylis glabra typica* near the west coast of Yamal Peninsula. Molluscs were dominant at St. 4387 and St. 3, where *Tridonta borealis* and *Serripes groenlandicus* were the most numerous. However, dominance of Polychaeta was obvious for the section in total (Figs. 4 and 7, from 40 to 80%).

Biomass had a similar general tendency. Near-shore areas are characterised by high biomass (more than 200 g/m^2), while biomass did not exceed 60 g/m^2 at stations 4389, 4387, 4385 in the open sea. (Fig.4).

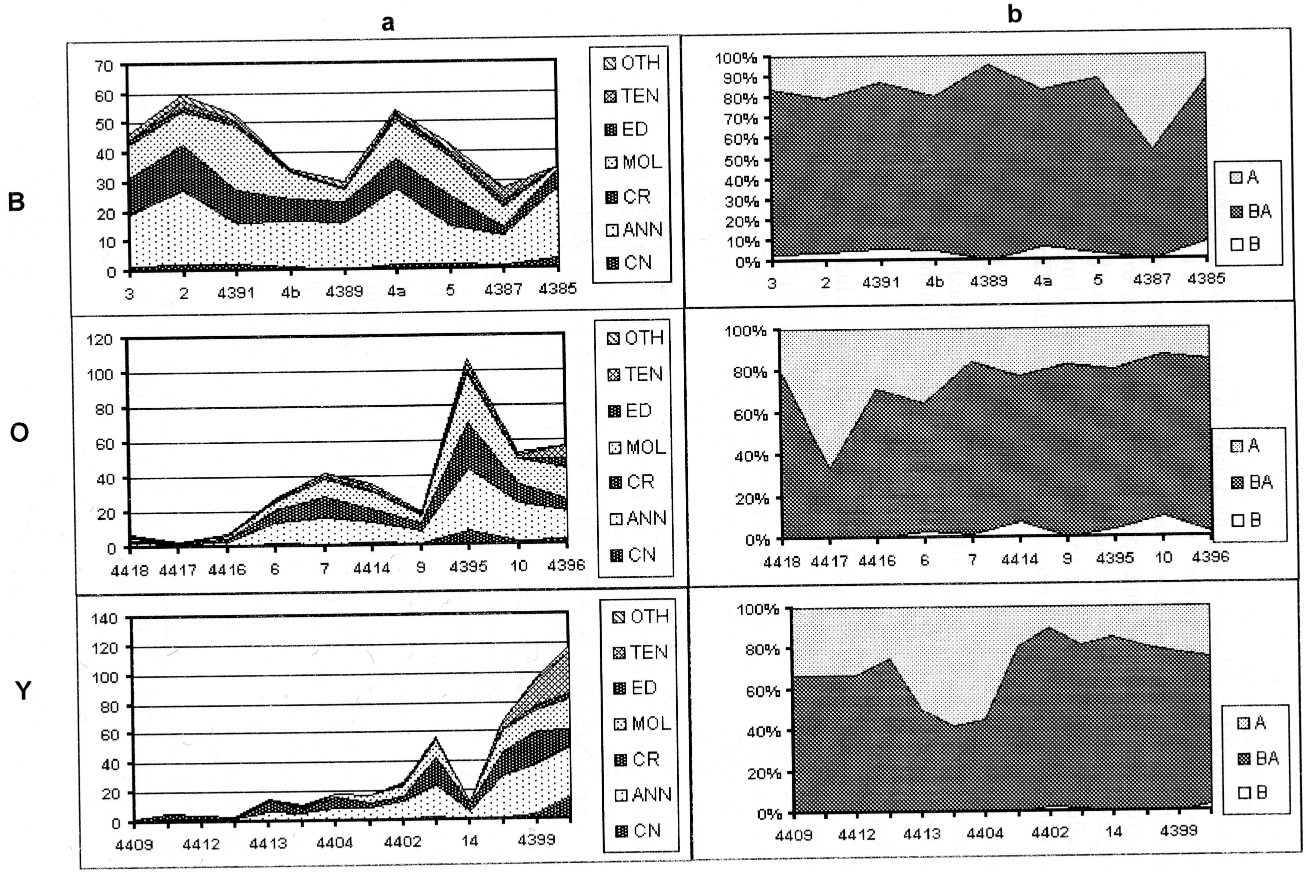

Fig. 3: Species richness (a) and biogeographical structure (b) of macro-zoobenthos along the Baydara (B), Ob (O) and Yenisei (Y) sections in the Kara Sea. A - Arctic; BA - Boreo-Arctic; B -Boreal; ANN - Annelida; CN - Coelenterata; CR - Crustacea; ED - Echinodermata; MOL - Mollusca; TEN - Tentaculata; OTH - Varia.

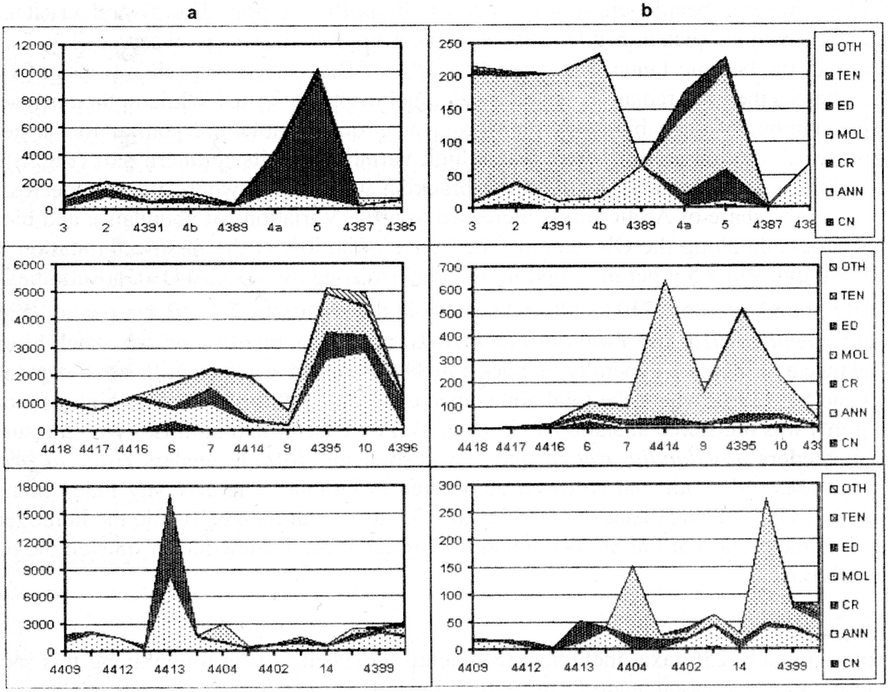

Fig. 4: Zoobenthos abundance (ind. m^{-2}) (a) and biomass (g m^{-2} wet weight) along the Baydara (B), Ob (O) and Yenisei (Y) sections. Other explanations: see Figure 3.

Bivalves formed highest biomass at the southern shallow stations, with the suspension filter feeders *Nicania montagui, Tridonta borealis* and *Macoma calcarea* predominating. Deposit feeding species (the crustacean *Diastylis glabra* and Holothuroidea) played a noticeable role in biomass only at St. 4a and 5 located near the coast of Yamal Peninsula.

Diversity increased from 2.56 to 4.79 from the open sea to the coastal stations in the South. The lowest diversity corresponds to the depression in the sea floor. The faunal homogeneity indexes show an opposite trend.

Ob section

Of the 260 taxa of the Ob section, 182 were identified to species level. At the southern station 4418, located opposite the Tasov Bay, freshwater species, including oligochaetes, mosquito larvae and bivalves were found; and species number did not exceed 20 in each replicate. To the North, in the northern part of the middle Ob Bay (at St. 4417), freshwater organisms were substituted by brackish water species. Numbers of species decreased to only 3-4 taxa in each replicate, mainly the polychaete *Marenzelleria arctia*, the amphipod *Pontoporeia affinis*, and the priapulid *Halicryptus spinulosus*.

Marine fauna was found only in the outer part of the bay, with gradually increasing depth. Under these marine conditions, the number of species increased northward up to106 taxa at mouth of the bay, the deposit feeder *Portlandia estuariorum* was dominant, while in the open sea the main part of biomass was formed by the deposit feeder *Macoma calcarea* and the suspension filter feeders *Nicania montagui* and *Musculus niger*. The lowest diversity of 0.69 was registered at St. 4412 in the estuarine area of the Yenisei Bay; and the highest diversity of 5.22 was marked at the most northern station 4398. The lowest monotony, at St. 11 in a small depression (U=0.13), was two times smaller than at the St. 4398, while the diversity index there (5.12) was practically equal to that at St. 4398.

3.3 Community structure

Cluster analyses allowed to identify 12 assemblages (Fig. 5). Table 2 lists the ten dominating species (with highest ranks in validity) and their abundances, biomass and validity values within the assemblages as well as general data. Patterns of distributions of the assemblages and geographical areas inhabited are shown in Figure 6.

4 Discussion

4.1 Species richness

The bottom fauna of the investigated southern areas of the Kara Sea, including the estuarine zones of the Yenisei and the Ob bays, comprised 498 taxa. However, the number of species may be greater by 25-35%, because such groups as sponges, nematodes, nemertines, pantopods, sipunculides and some cnidarians were not identified to species level. The recorded species list is 2.5 times greater than the list published by Antipova and Semenov (1989), which can be explained by using different approaches for identification of species and different sampling procedures. Neverthless, the main part of the species belongs to crustaceans (28%), polychaetes (26.5%) and molluscs (21.5%) in 1993 as well as in 1975 (Antipova, Semenov, 1989) and in 1997 and later (Poltermann et al., 1999; Deubel et al., this volume). The strong influences of fresh water runoff exclude stenohaline organisms from the inshore areas and prevents the penetration of typical marine animals to the central and the inner parts of the Bays (see also Deubel et al., this volume). In spite of the raised species numbers in our evaluations, our total species number is approximately two times lower than in studies of the neighbouring part of the Barents Sea, the Pechora Sea (Denisenko et al. 1997, Dahle et al. 1998), performed by similar methods. This lower species richness in the Kara Sea can be explained by the more severe environment. Actually, the number of taxa varied from 3 to 137 per 0.5 m^2 in different samples. On average, diversity was greater in the western than in the eastern study area (Fig. 7, species numbers). The differences between the rich inshore areas of the south-western part of the Kara Sea and the very poor fauna in the estuarine areas of the Ob and Yenisei bays are explained by more severe and variable environmental conditions in the estuaries, and firstly, by the differences in salinity fluctuations (see also Leschiskaya, 1962, Remane and Schlieper, 1971, Cochrane et al., 1997, Poltermann et al., 1999).

4.2 Biogeography

The strong influence of the Arctic environmental conditions is reflected in the biogeographic structure of the zoobenthos of the Kara Sea, with dominance of the Boreal-Arctic forms, which comprised 68.5% or 261 species. Arctic forms comprise 97 species

(26%), and their portion increases gradually from the West to the East and North (see Filatova, 1957).

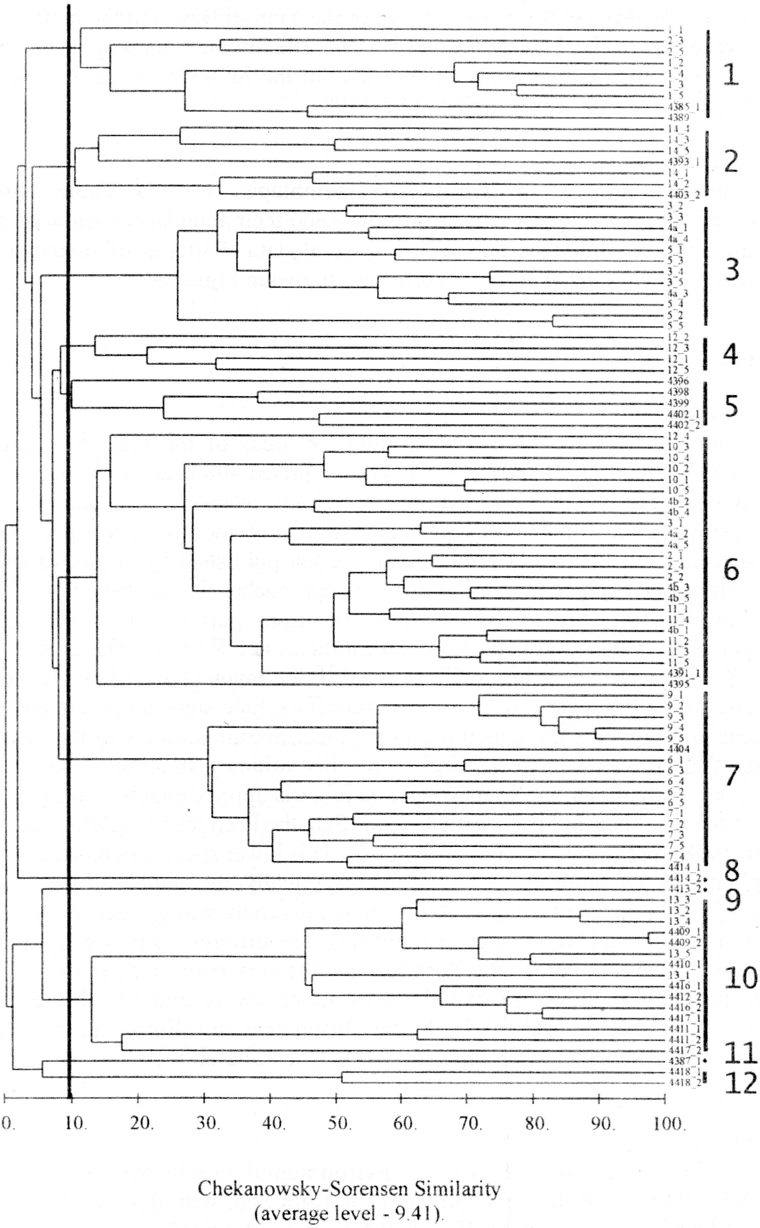

Fig. 5: Cluster dendrogram, showing the grouping of stations, based on percent of similarity of the "relative production" of macro-zoobenthos. 1 – 12: communities as in Table 2.

Table 1: Station positions, depths and sediments in the study area of the Kara Sea.

R/V*	Station	Section**	Latitude - North	Longitude - East	Depth (m)	Sediment
DZ	1	B	70° 00'	61° 41'	195	silty mud
DZ	2	B	69° 39'	65° 36'	30	sandy mud
DZ	3	B	69° 19'	66° 14'	24	sandy mud
DZ	4a	B	70° 00'	66° 00'	23	muddy sand
DZ	4b	B	70° 39'	65° 29'	32	sandy mud
DZ	5	B	70° 59'	65° 49'	23	muddy sand
DZ	6	O	72° 30'	74° 25'	17	silty mud
DZ	7	O	72° 59'	72° 58'	28	silty mud
DZ	9	O	73° 58'	73° 17'	30	silty mud
DZ	10	O	74° 27'	73° 17'	26	muddy sand
DZ	11	Y	74° 18'	78° 34'	31	muddy sand
DZ	12	Y	72° 25'	80° 39'	43	sandy mud
DZ	13	Y	73° 35'	80° 06'	20	silty
DZ	14	Y	73° 54'	81° 03'	41	silty
DM	4385	B	73° 20'	64° 35'	117	silty
DM	4387	B	72° 00'	64° 35'	150	silty
DM	4389	B	70° 30'	64° 34'	105	clayey mud
DM	4391	B	69° 46'	64° 51'	45	clayey mud
DM	4393	B	70° 23'	63° 05'	216	sandy mud
DM	4395	O	74° 14'	73° 00'	30	sandy mud
DM	4396	O	75° 00'	73° 00'	35	clayey mud
DM	4398	Y	76° 00'	80° 00'	55	sandy mud, gravel
DM	4399	Y	75° 00'	80° 00'	40	muddy clay
DM	4402	Y	73° 30'	80° 00'	38	sandy mud
DM	4403	Y	73° 00'	80° 00'	24,5	sandy mud
DM	4404	Y	72° 30'	80° 00'	20	sandy mud
DM	4409	Y	71° 20'	82° 59'	22	silty
DM	4410	Y	71° 36'	83° 19'	21	silty
DM	4411	Y	71° 49,6'	82° 37'	29	silty
DM	4412	Y	71° 48,7'	83° 10.4'	22	sandy mud
DM	4413	Y	72° 11,5'	82° 24.1'	13	sandy mud
DM	4414	O	73° 49,9'	73° 30'	26	silty
DM	4416	O	71° 45'	73° 09'	18	sandy mud
DM	4417	O	70° 56,8'	73° 33.9'	20	sandy mud
DM	4418	O	68° 49,6'	73° 40.6'	13	sandy mud

*DZ = "Dal'niye Zelentsy; DM = "Dmitriy Mendeleev"
** B =Baydara Section, O = Ob Section; Y = Yenisei Section

The Boreal forms comprise only 17 species or 3% of the total fauna, mainly represented by widespread and Amphiboreal species. In contrast to the distribution of Arctic species, the share of Boreal forms decreases from the South-West to the East and North. (Fig. 7)

4.3 Abundance and biomass

Variations of the quantitative characteristics of zoobenthos correlate with the changes in species composition (Figs. 3, 4, 7). Thus, the strong S-N-gradient in biomass and abundance in the Baydara section reflects more a negative influence of unsuitable muddy sediments and flow of food than of the water regime.

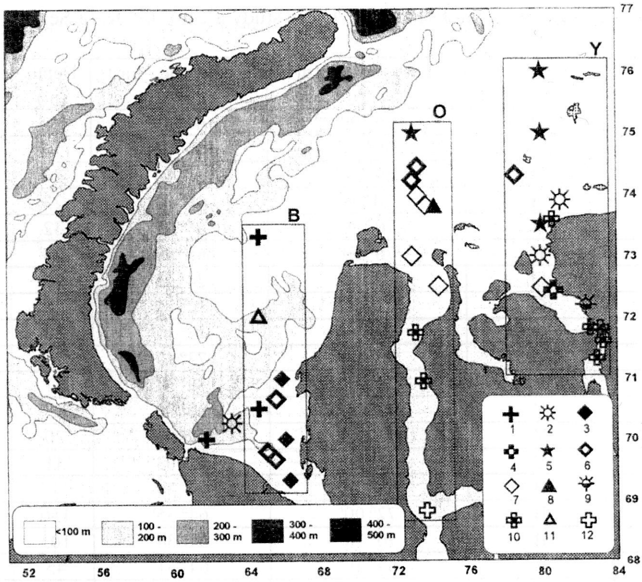

Fig. 6: Benthic communities distribution in the study area in 1993. Names of clusters according to their numeration are the same as in Table 2.

The lowest biomass in the northern part of the Baydara section (near the Novaya Zemlya Trough), corresponds to soft silt-clay sediments. Along the Ob and Yenisei transects, however, differences in other environmental conditions such as the hydrological regime, salinity, decreases of temperature, increasing depths in combination with the presence of suitable sediments and food supply (Romankevich and Vetrov, 2001), agree with the variation in biomass distribution. In both bays, a noticeable increase of zoobenthos diversity, density and biomass is observed at stations, where bottom salinity exceeds 25. Nevertheless, local rises of zoobenthos biomass are also found when salinity varies from 7-8 up to 20.

The comparison of the data collected in 1993 and 1997 (Poltermann et al. 1999) with the results of previous studies shows similarities of biomass distribution in the Ob Bay. In the 1950s (Leschinskaya, 1962) and 1980s (Kusikova, 1989), the mean total biomass varied from 3.3 to 4.4 g per m^2 in the central and from 10 to 12 g per m^2 in the mouth of the bay. According to Leschinskaya (1962), the strong seasonal variation of the hydrological regime provokes strong fluctuations of zoobenthos biomass in the bay. In winter, the outflow of the Ob is decreased, and salinity in the study area increases, enabling the immigration of brackish-water animals and causing reductions and disappearances of fresh-water animals.

Any comparable former publications about the bottom fauna were not found for the Yenisei Bay; but, its similarity (with strong seasonal variations of environmental conditions) suggests similar annual fluctuations in the quantitative characteristics of the bottom fauna. The high biomass (200-300 g m^{-2} or 7.0 -10.3 g C_{org}) in the inner part of the Baydara Bay is comparable to values published by Filatova and Zenkevich (1957), Antipova and Semenov (1989), Denisenko et al. (1993), though Kiyko and Pogrebov (1997) reported biomasses of about 100 g m^{-2}. The intensive circulation and inflow of organic matter from the Pechora Sea promote the development of rich benthic communities, although primary production and direct organic flux seem to be relatively low in Baydara Bay (Vedernikov et al., 1995; Lebedeva and Shushkina, 1995).

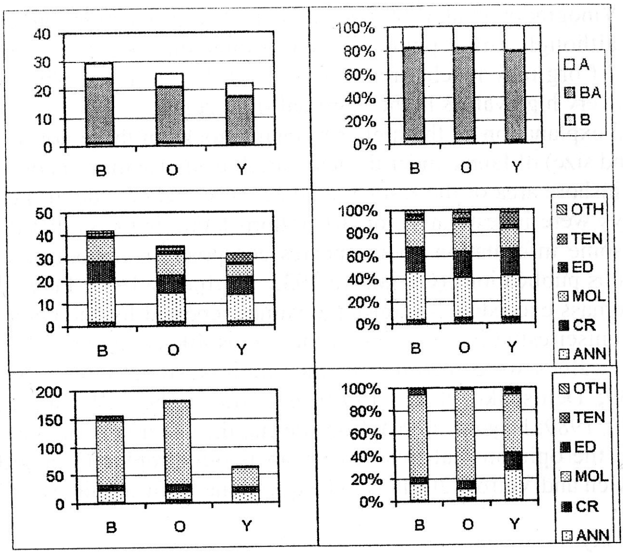

Fig. 7: Comparison of the biogeographic stucture (a), mean species number on 0.5 m^2 (b) and gross wet biomass (g m^{-2}) (c) of the 3 sections. Other explanations: see Figure 3.

The higher zoobenthos biomass near the Yamal Peninsula is possibly caused by the presence of ice-free water during the whole year (Atlas of the Oceans, 1980), which ensures the normal cycle of the primary production of phytoplankton communities (Drujkov and Drujkova, 1998; Makarewich, 1998; Kusnetsov and Drujkov, 1997; see also Romankevich and Vetrov, 2001).

In spite of high concentrations of dissolved and suspended organic matter in the water column in the inshore area in front of the mouths of the Ob and Yenisei Bays (Lisitzin, 1995; Romankevich and Vetrov, 2001), the biomass of zoobenthos was characterised by intermediate values (50-80 g m^{-2} or 1.8-2.8 g C_{org} m^{-2}). The same order of magnitude was registered in 1997 (Poltermann et al. 1999; Deubel et al., this volume). This discrepancy can partly be explained by the high portion of unsuitable refractory organic matter, advected with the river discharge e.g. from tundra soils. It is also possible that high concentrations of suspended inorganic matter (Kuptsov et al., 1994) and of yellow substances hinder primary producers and, hence, the development of a very rich bottom fauna. In the northernmost parts of the Ob and Yenisei sections, however, the biomass amounts to 650 and 270 g m^{-2} (21.9 and 9.23 g C_{org} m^{-2}), though Kiyko and Pogrebov (1997) described biomass of about 100 g/m^2. A similar contrast was observed in the plankton community, where calanoids were unusually abundant in traps (Lisitzin et al., 1995) in spite of the low primary production during the investigated autumn time (Vedernikov et al. 1995). According to Kusnetsov and Druzhkov (1997), the advection of phytoplankton from neighbouring polynyas (Makarevich 1998) may also happen in this northern area. This can at least partly explain the higher biomass of zoobenthos at the northern stations of the Ob - Yenisei - sections. However, Vinogradov et al.

(1995; see also Lisitzin, 1995) noted that the Kara Sea can not be classified as a basin with high productivity, although satellite images sometimes indicate high chlorophyll concentrations. Vinogradov et al. (2000) discussed a low production rate of phytoplankton in the Kara Sea although chlorophyll concentrations may be high; on the other side, sedimentation of Corg may reach values 30-85% of the produced phytoplankton matter in September, with very high values in the marginal filter zones.

An additional explanation of the higher biomass stocks in these northern section areas is the longevity (and size) of fauna under the less variable environmental conditions there.

The shallow inshore area of the Kara Sea adjacent to and outside of the mouths of the Ob and Yenisei Bays were investigated for the bottom fauna biomass distribution for the first time, although some information about species composition for both areas was presented already in previous publications (Gurjanova 1933; Gorbunov 1937; Pergament 1945). Inside the estuaries, biomass exceeded 2-3 times the values reported for the Ob and in 10 times the values of the Yenisei estuarine sections in the 1930s-40s (Filatova and Zenkevich, 1957). Similar biomass values were recorded in the south-western Barents Sea (Brotskaya and Zenkevich, 1939; Denisenko et al., 1999) and the offshore Bering and Chukchi Seas (Grebmeier, et al., 1989; Dayton, 1990). Considering the apparently high zoobenthos biomass in the Kara Sea, the opinion that this ecosystem is oligotrophic (Vinogradov et al., 1995, 2000; Romankevich and Vetrov, 2001) is to be questioned to a certain extent.

4.4 Species diversity

The Shannon diversity index variations reflect the natural variations of the bottom community structures along the sections as a result of the heterogeneous, partly critical salinity and sediment conditions. Such unfavourable environments as in the estuaries assist to decrease the diversity and to increase the level of the homogeneity of the zoobenthos communities along the bay sections. The lowest diversity was registered in these brackish water zones (0.41 and 0.69 respectively in the Ob and Yenisei bays), while diversity varied from 2.56 to 5.35 in the open sea. A similar trend is also described by Deubel et al. (this volume).

Low values were found in bottom depressions, high values in areas with mixed sediments. Similar diversity variations were registered in the Pechora Sea (Dahle et al., 1998). This confirms again that the Kara Sea is not to be generally regarded a poor basin, especially as the echinoderms predominate over other animals in offshore waters according to Zenkevich (1963) and Deubel et al. (this volume).

4.5 Community structure

The identification and characterization of benthic associations has traditionally been based on either abundance (Petersen, 1914) or biomass (Moebius, 1877). The "relative production value" calculated by us from data on both, abundance and biomass, allows for a wider consideration of functional roles of individual species in a benthic community (Denisenko et al. 1993; Kucheruk, 1995). A similar approach to assess the importance of different populations was taken by Kucheruk et al. (1998) in the south-western Kara Sea. The advantage of the "relative production method" is that it balances the impact of (1) numerous small-bodied organisms as well as (2) single large individuals of one or a few species present in a single sample. Using "relative production values" enables also a consideration of samples collected throughout the year, including periods of mass larval settlement, without causing major changes in the dominance relationships within a community.

Table 2: Bottom communities of the southern Kara Sea with data on the ten most important species.

Community	N samples	N species	Average similarity of samples within group, %	Average community biomass, g/m^2	Species	Average abundance[1], ind./m^2	Average biomass, g/m^2	Frequency in samples set	Species significance %
1	2	3	4	5	6	7	8	9	10
1[2]	9	165	41.77	243.8	***Spiochaetopterus typicus***	240	89.248	1.00	75.7
					Bathyarca glacialis	102	41.400	0.56	6.28
					Laonice cirrata	32	16.566	1.00	5.4
					Thyasira gouldi	185	2.495	0.89	2.47
					Maldane sarsi	50	5.634	0.89	2.38
					Yoldia amygdalea	65	52.765	0.22	1.44
					Nuculana pernula	15	4.243	0.67	1.37
					Yoldiella lenticula	141	2.548	0.67	1.17
					Yoldiella fraterna	370	1.736	0.56	0.96
					Hamingia arctica	15	102.150	0.22	0.85
2	7	46	18.51	26.1	***Saduria sabini***	14	20.370	0.57	51.8
					Aglaophamus malmgreni	9	3.199	0.43	15
					Cirratulidae spp.	106	0.485	0.71	14
					Yoldiella sp.	185	1.050	0.29	5.29
					Micronephthys minuta	116	0.059	0.86	3.94
					Yoldiella intermedia	87	1.007	0.43	3.69
					Tauberia gracilis	114	0.090	0.71	2.85
					Aricidea g.sp.	112	0.038	0.86	2.5
					Terebellides stroemi	7	0.228	0.29	0.79
					Scalibregma inflatum	10	0.100	0.29	0.14
3	12	155	41.16	202.0	***Serripes groenlandicus***	27	119.763	1.00	67
					Diastylis glabra typica	7201	39.317	0.58	12.7
					Stegophiura nodosa	246	8.133	0.92	8.08
					Leitoscoloplos sp	90	1.864	0.92	2.37
					Cirratulidae spp.	192	0.687	1.00	1.91
					Myriotrochus rinkii	12	5.980	0.50	1.36
					Cucumaria calcigera	25	24.770	0.33	0.94
					Macoma calcarea	18	4.388	0.42	0.89
					Ophiocten sericeum	22	4.818	0.33	0.64
					Elliptica elliptica	80	29.400	0.17	0.61
4	4	93	19.68	41.0	***Praxillella praetermissa***	27	5.297	0.75	37.8
					Ophelina acuminata	10	4.079	0.75	14.6
					Terebellides stroemi	15	1.304	1.00	12.1
					Macoma calcarea	15	6.680	0.50	10.8
					Cirratulidae spp.	95	0.431	1.00	6.38
					Tauberia gracilis	158	0.073	1.00	3.9
					Micronephthys minuta	185	0.098	1.00	3.57
					Yoldiella intermedia	130	1.270	0.50	2.59

Table 2: cont.1

1	2	3	4	5	6	7	8	9	10
					Scalibregma inflatum	13	7.003	0.75	2.06
					Pectinaria hyperborea	10	2.433	0.50	1.62
5	5	214	26.56	57.4	***Ophiocten sericeum***	65	6.463	1.00	33
					Aglaophamus malmgreni	27	8.168	0.80	18.5
					Tridonta borealis	4	8.611	0.60	11.1
					Cirratulidae g.sp.	300	0.746	1.00	7.46
					Portlandia arctica	32	4.311	0.60	6.33
					Terebellides stroemi	37	1.585	0.80	4.39
					Maldane sarsi	268	8.856	0.40	4.2
					Nuculana pernula	5	3.327	0.60	3.8
					Phascolion strombi	32	2.755	0.60	3.4
					Musculus laevigatus	8	4.966	0.40	2.03
6	24	305	38.49	253.4	***Tridonta borealis***	75	133.487	0.92	60.1
					Macoma calcarea	62	38.589	0.83	17.2
					Maldane sarsi	191	11.016	0.67	4.38
					Nicania montagui	119	34.367	0.58	3.74
					Cirratulidae spp.	345	1.934	0.92	3.33
					Yoldia amygdalea	50	7.212	0.50	1.19
					Portlandia arctica	58	15.135	0.29	1.14
					Terebellides stroemi	58	1.096	0.88	1.01
					Leitoscoloplos sp	62	0.616	0.83	0.93
					Lumbrinidae g.sp.	52	3.551	0.67	0.88
7	17	146	43.69	125.9	***Portlandia arctica***	278	63.643	1.00	83.8
					Yoldiella intermedia	400	3.918	0.65	4.79
					Terebellides stroemi	34	4.822	0.82	2.69
					Pectinaria hyperborea	27	7.687	0.41	1.61
					Musculus niger	28	20.059	0.29	1.34
					Saduria sabini	17	15.896	0.41	0.94
					Cerianthus lloydi	284	25.230	0.29	0.78
					Macoma calcarea	39	16.598	0.24	0.71
					Ampharetidae spp.	285	0.805	0.47	0.57
					Diastylis sulcata	118	0.769	0.41	0.4
8	1	53		1152.6	***Hiatella arctica***	316	621.03		
					Musculus niger	256	388		
					Musculus corrugatus	1176	36.46		
					Saduria sabini	8	41.96		
					Nereis zonata	48	8.136		
					Saduria sibirica	4	13.76		
					Actiniaria g.sp.	16	6.44		
					Portlandia arctica	184	2.816		
					Ciliatocardium ciliatum	4	8.96		
					Chone infundibuliformis	4	6.16		

Table 2: cont.2

1	2	3	4	5	6	7	8	9	10
9	1	15		53.2	*Pontoporeia affinis*	8032	32.54		
					Oligochaeta g.sp.	8164	12.164		
					Onisimus botkini	320	5.124		
					Saduria entomon	24	1.724		
					Onisimus sp.	320	0.288		
					Marenzelleria arctica	84	0.32		
					Halicryptus spinulosus	4	0.448		
					Capitella capitata	12	0.22		
					Ampharete vega	4	0.138		
					Nematoda g.sp.	100	0.04		
10	15	37	57.49	24.1	***Marenzelleria arctica***	718	13.657	1.00	88.3
					Saduria entomon	8	5.767	0.60	5.05
					Pontoporeia affinis	423	2.806	0.40	3.69
					Minispio cirrifera	382	3.936	0.33	1.89
					Nemertini g.sp.	11	0.165	0.53	0.3
					Halicriptus spinulosus	10	5.158	0.33	0.29
					Oligochaeta g.sp.	344	0.204	0.33	0.24
					Ampharete vega	32	1.737	0.20	0.15
					Diastylis sulcata stuxbergi	78	0.325	0.27	0.07
11	1	27		5.8	***Yoldiella lenticula***	80	2.448		
					Scalibregma inflatum	92	0.652		
					Bivalvia g.sp.	92	0.556		
					Yoldiella sp.	176	0.352		
					Yoldiella fraterna	96	0.240		
					Escharoides jacksoni	8	0.440		
					Golfingia sp.	100	0.100		
					Ophiocten sericeum	4	0.236		
					Aglaophamus malmgreni	4	0.156		
					Lumbrinereis sp.	20	0.076		
12	2	14	73.97	1.7	***Oligochaeta g.sp.***	650	1.179	1.00	
					Spirosperma ferox	396	0.248	1.00	
					Bivalvia g.sp.	164	0.332	0.50	
					Tendipedidae g.sp.	26	0.050	1.00	
					Pisidium sp.	16	0.060	0.50	
					Nematoda g.sp.	20	0.010	1.00	
					Bowerbankia arctica	4	0.036	0.50	
					Bathyarca sp.	4	0.024	0.50	
					Yoldiella fraterna	12	0.008	0.50	
					Copepoda g.sp.	14	0.005	1.00	

[1] Average abundance and biomass of species are calculated for the whole determined community.
[2] Number of community corresponds to the number of cluster on Figures. 5 and 6.

Comparison of the present results on community structures based on "relative production values" with previously published data based on biomass (Filatova and Zenkevich, 1957; Antipova and Semenov, 1989; Jørgensen et al., 1999; Kiyko and Pogrebov, 1997) reveals some dissimilarities. In the present study the importance of large-sized animals is reduced, the number of communities in the offshore area is smaller, and their spatial dispersal differs markedly in some cases. However, the early determination of communities in the Kara Sea was not based on sufficiently statistical analyses. Furthermore, the area of distribution of each community was assumed to follow the isolines of bottom topography, but taking them into account only roughly. Although the net of stations in our study does not cover the area equally and sufficiently, the 12 communities (clusters) described here have obvious general similarities in their distribution with patterns shown in the literature (Filatova and Zenkevich, 1957; Kusikova, 1989). Cluster analyses displayed two communities in the estuarine zones, as found in the Ob Bay area by Kusikova (1989). Filatova and Zenkevich (1957) registered five communities in the more open parts the Sea. We found 6 clusters there, and their distribution and dominant species do not completely correspond with the previous results. On the other hand, our finding differ more considerably from results published in the 1980s (Antipova and Semenov, 1989), who found six communities in the Baydara Bay and nearby areas. Filatova and Zenkevich (1957) and Antipova and Semenov (1989) stressed the predominance of echinoderms in the Kara Sea; and echinoderm-dominated communities occupied considerable parts of the Kara Sea in the 1940s and 70s. Such a predominance of echinoderms was not determined on our material; however, this seems to occur north of about 74° according to Deubel et al. (this volume).

According to our results the association of *Spiochaetopterus typicus* substituted that of *Ophiopleura borealis* (Filatova and Zenkevich, 1957; or of *Ophiocten sericeum* according to Antipova and Semenov,1989, or Ophiurids - Kiyko and Pogrebov, 1997). The discrepancy may be caused, first, by the different approach in the sampling of zoobenthos. Filatova and Zenkevich (1957) based their description mainly on trawling data, and, thus, not so much on infauna. Only two stations (within their community of *Ophiopholis aculeata*) comprised analyses from Ocean grab samples. *S. typicus* is reported as the dominant species near the Vaygach Island only. However, beside the predomination of *O. borealis* they also noted a mass population of *S. typicus* on the slope of the Novaya Zemlya Trench in their *Ophiopleura borealis* community. In 1993, the boundaries of the *Spichaetopterus typicus* community had moved to the north-west and were restricted the Novaya Zemlya Trench.

In the inner part of the Baydara Bay and near the western coast of the Yamal Peninsula we found an association of *Serripes groenlandicus* instead of the community of *Portlandia arctica* (sensu Filatova and Zenkevich, 1957). The *S. groenlandicus* community was marked already in 1990-1991, too (Denisenko et al., 1993; Kiyko and Pogrebov, 1997).

Our results about the distribution of the community of *Tridonta borealis* agree with those of Filatova and Zenkevich (1957), Antipova and Semenov (1989), Denisenko et al. (1993), and Kiyko and Pogrebov (1997). All studies document the predominance of *T. borealis* outside the Baydara Bay. In the less investigated north-eastern part of the southern Kara Sea our results agree also with observations in the 1930-1940s (Filatova and Zenkevich, 1957).

A main reason for the disagreement between the dominant species in the communities and in their distribution is the different methodological approach to analyse bottom biocenoses. As discussed above, in our case, not only biomass, but also abundance is taken into account to compute the "relative animal production" and, thus, to better account for possible multiannual fluctuations in community structures. In addition, we have to keep in mind that by using grabs only, large echinoderms like the brittle star *Ophiopleura borealis* are under-represented in our samples, while they are over-estimated by dredging. Whether climate fluctuations have also contributed to the registered zoobenthos changes of the Kara Sea, is a question to be answered by future investigations. Taking into account the quality and quantity of material used for the description of biomass distribution of zoobenthos and the determination of the boundaries of bottom communities, quite approximate pictures of both benthos characteristics were published by Filatova and Zenkevich (1957) and by Kiyko and Pogrebov (1997). However, they demand revising and verification. The distribution of assemblages given in Deubel et al. (this voulme) is also regarded as preliminary, as it shows the general trends from Ob and Yenisei estuaries up to the central Kara Sea, but not all very details.

Besides of resemblance of the structure of the majority of bottom communities within the Kara Sea described in all periods of observation, the present results also demonstrate similarities of the community structures in the western part of the Kara Sea with those in the Pechora Sea. In both areas, the community dominated by *Serripes groenlandicus* was recorded in shallow waters, while depths of more than 40 m are inhabited by the community of *Tridonta borealis* and the soft sediments in deeper parts of the seas by that of *Spiochaetopterus typicus* (Denisenko et al. 1997).

5 Conclusions

The benthic fauna of the Kara Sea is strongly influenced by abiotic factors, such as depth, water masses, temperature, salinity and sediment granulometry, and by their variability. Despite the differences in methodological approaches and the interval of 50 years between observations, the general main trends recorded in the distribution of macro-zoobenthos communities are similar in all benthic investigations. The high biomass in offshore parts of the Sea is inconsistent with the opinion that oligotrophic environmental conditions characterize the Kara Sea, and additional efforts are needed to clarify this discrepancy.

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