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ORIGINAL PAPER

Zoobenthos of the Cheshskaya Bay (southeastern Barents Sea): spatial distribution and community structure in relation to environmental factors

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Abstract Structural and functional characteristics of zoobenthos of the Cheshskaya Bay (SE Barents Sea) were studied at 21 stations in June/July 1995. Strong prevailing cyclonic and tidal currents result in relatively uniform temperature and salinity in the area. Sediments consist mainly of sand and pebbles, while the flux of suspended matter from rivers locally increases the share of finer fractions. Analysis of species composition (419 taxa), abundance (up to 4,200 ind m^{-2} and up to 29,000 ind m^{-2} with juveniles) and biomass (up to >6,000 g wet wt m^{-2}) indicates high species richness in most parts of the bay, especially in the northeast. Analysis of community structure using production characteristics of species revealed a general predominance of suspension feeders partitioned into seven communities. The dominant species of these communities were *Mytilus edulis* and *Balanus crenatus* (Type 1), *B. crenatus* (Type 2), *Modiolus modiolus* and *Verruca stroemia* (Type 3), *Flustra foliacea* and *V. stroemia* (Type 4), *Hydrallmania falcata* (Type 5), *V. stroemia* and *Chirona hameri* (Type 6), and *Ophelia limacina* (Type 7). The structure of the communities is mainly regulated by sediment type, water depth and, to some extent, by riverine input.

Keywords Zoobenthos · Abundance · Biomass community and trophic structure · Cheshskaya Bay · Barents Sea

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Introduction

Owing to its unique geomorphology, the Cheshskaya Bay (SE Barents Sea) differs noticeably from other embayments in the Barents Sea. Several geologic and oceanographic investigations in the region since the first decades in the early twentieth century showed that its sediments consist mainly of well-sorted sands, gravel and pebbles with variable, but relatively small portions of mud (Klenova 1929; Tarasov 1974), as result of the permanent cyclonic current strengthened by the influence of tidal currents (Lednev 1945). The high concentration of suspended organic carbon in the bay originates from river discharges (Garkavaya and Posdnyakova 1968; Medvedev and Potechina 1986).

The earlier zoobenthic studies were mostly descriptive (Gurjanova 1929; Brotskaya and Zenkevich 1932; Pushkin 1968) or examined only specific taxonomic groups (Gostilovskaya 1968; Rjepishevskiy 1968). According to these studies, zoobenthic structure and distribution were considerably different from those observed elsewhere in the Barents Sea. The major part of the sublittoral zone of the bay was occupied by suspension and deposit feeders with the presence of an estuarine species complex close to river mouths in the south-eastern portion of the Bay and intertidal zone (Gurjanova 1929; Pushkin 1968) in contrast to other sill/bounded bays of the Barents Sea where deposit feeders occupy a much larger area, especially in the depressions behind the sill (Golikov et al. 1993; Denisenko et al. 1999). Two views of the distribution of zoobenthos in the deeper part of the Cheshskaya Bay can be found. According to Brotskaya and Zenkevich (1932) the sublittoral zone of the bay is occupied by a single community type predominated by mussels, while Pushkin (1968) considered two community types, one predominated by brachiopods in the central part close to the entrance of the bay, and the other dominated by mussels, fringing the brachiopod community type.

In the late 1980s, general interest in the Russian Arctic increased drastically because of to the discovery of extensive oil and gas fields, and plans for the construction of an oil terminal in the Cheshskaya Bay. Related to this, multidisciplinary environmental studies by Murmansk Marine Biological Institute (MMBI) and Finnish Institute of Marine Research (FIMR) were carried out in 1995. Because of limited data and dissimilarity of earlier results described above, our research focused on the macrozoobenthic distribution, abundance and biomass in the Cheshskaya Bay with a special emphasis on diversity, community types and their trophic structure. Compared to previous investigations, our sampling contained a more extensive station grid covering the entire bay. This sampling strategy allowed for analyses of community variability and distribution within the bay, and examination of their relationships with environmental factors (depth, temperature, salinity and sediment type). Since the Cheshskaya Bay is among the ten most important areas in the Barents Sea as far as species diversity and the presence of relict boreal fauna are concerned, it is recommended to be a protected area (Larsen et al. 2004), and as such the information obtained in the present study is pertinent.

Study area

The Cheshskaya Bay is one of the largest bays in the Barents Sea (Fig. 1). Because of the lack of sills, a water exchange with the open sea is relatively unrestricted, generating typical marine characteristics (e.g. high salinity) in the whole bay. A prevailing strong cyclonic inflow current entering from the northern side of the bay (Lednev 1945) together with wind-induced and tidal currents create an intensive circulation of water masses. The shape of the bay, including a uniform gradual deepening towards the central basin, creates a current pattern superimposed by the tide (max. tidal range. 6 m; Terziev 1992) that thoroughly mixes the coastal waters, causing marked shore erosion and turbid waters. The concentration of suspended inorganic matter in the water decreases towards the central part (from 5–10 to 2–3 mg l^{-1}; Medvedev and Potechina 1986). These specific hydrodynamic features jointly with a bottom morphology lacking marked depressions suitable for sedimentation of fine-grained material lead to a predominance of hard sediments with sands of medium and coarse grain size and variable fractions of gravel (Tarasov 1974). Soft bottoms with silt and sandy silt are found only close to the Pesha, Chesha and other river mouths and in some shallow areas in the southern part at depths of 5–7 m (Pushkin 1968; Tarasov 1974).

Freshwater inflow from the numerous small rivers (in total ca. 5.3 km^3 $year^{-1}$, in comparison with 156 km^3 $year^{-1}$ recorded in the neighbouring Pechora River; Terziev 1992) has a marked effect on hydrography only in the southeastern part of the bay. Due to current pattern, the water column of the bay is practically non-stratified (i.e., homohalinic and -thermic) throughout the year. Because of efficient mixing, the near-bottom levels of dissolved oxygen are favourable for benthic life all year round (95–105% of full oxygen saturation; Garkavaya and Posdnyakova 1968). During the summer, salinity (PSU) in the central deeper region varies between 29.50 and 34.36 (Table 1), while in winter it may reach 36 due to the decrease in freshwater inflow and ice cover formation (Brotskaya and Zenkevich 1932; Garkavaya and Posdnyakova 1968). The bay is completely covered by ice between October and March, and extensive ice fields remain until mid-July (Garkavaya and Posdnyakova 1968; Rjepishevskiy 1968; Gorshkov 1980). Under the ice, cold surface water (down to –1.8°C) remains from March until mid-May. The warmest period is late August with seawater temperatures around 14°C, which is unusually warm compared to most other parts of the Barents Sea where water temperature does not exceed 9°C (Terziev 1992). The main growth period of microalgae extends from early April (under the floating broken ice; Garkavaya and Posdnyakova 1968) to late August (Vinogradov et al. 2000). High primary production characterises this period, with mean daily values from 100 mg C m^{-2} day^{-1} in the western part to 1,000 mg C m^{-2} day^{-1} in the eastern part of the bay (Vinogradov et al. 2000).

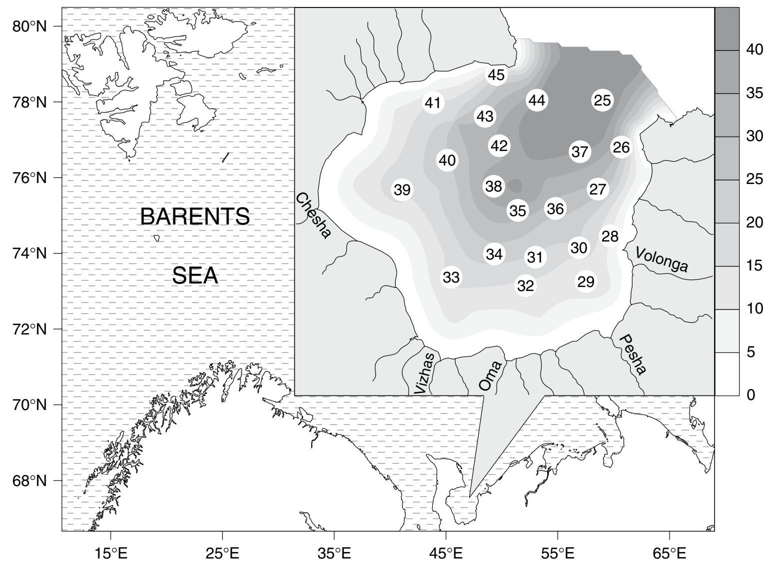

Fig. 1 Map of the study area and zoobenthos sampling station network in the Cheshskaya Bay in 1995. Depth scale in meters

Table 1 Sampling stations in the Cheshskaya Bay, with background information

Station number	Depth (m)	Samples (*n*)	Latitude (deg N)	Longitude (deg E)	*S* (PSU)	*T* (°C)	Sediment description
25	49.2	1	67.68	47.47	33.05	4.12	Stones, sand
26	30.6	3	67.53	47.66	31.45	6.57	Sand, stones
27	27.8	4	67.39	47.45	32.05	7.65	Coarse sand, stones, broken shells
28	11.8	4	67.24	47.55	29.50	10.25	Coarse sand, stones, shells
29	14.3	5	67.19	47.50	32.15	10.21	Stones, pebbles, gravel sand
30	19.9	4	67.19	47.27	32.35	8.81	Stones, coarse sand
31	19.4	4	67.16	46.88	34.36	8.42	Fine and coarse sand, pebbles
32	13.8	2 + 2 PG	67.07	46.78	34.21	8.92	Fine and coarse sand, pebbles
33	17.2	4	67.09	46.12	33.60	7.52	Coarse sand, broken shells
34	22.2	3 + 1 PG	67.18	46.50	33.95	7.42	Gravel, sand, broken shells, pebbles
35	32.8	4	67.32	46.72	33.69	7.18	Fine sand, pebbles, stones
36	27.2	4	67.33	47.05	32.95	6.71	Sand, broken shells, stones, pebbles
37	38.8	4	67.51	47.28	32.60	5.44	Fine sand, shells, stones, pebbles
38	39.7	4	67.40	46.50	33.75	6.03	Pebbles, shells, sand
39	21.6	4	67.38	45.68	33.60	6.70	Broken shells, shells, stones
40	23.4	4	67.48	46.08	33.40	6.07	Broken shells, muddy sand, stones
41	17.7	4	67.67	45.95	33.01	5.55	Muddy fine sand, shells, stones
42	35.7	4	67.32	46.33	–	–	Fine sand, shells
43	29.9	4	67.63	46.43	33.15	5.64	Muddy fine sand, stones
44	38.4	2	67.68	46.88	32.50	6.14	Muddy fine sand, stones, shells
45	20.0	4	67.47	46.31	–	–	Muddy sand, stones, broken shells

PG Petersen grab, – missing data, *S* near-bottom salinity, *T* near-bottom temperature

Methods

Field and laboratory work

Zoobenthic sampling was conducted in June–July 1995 aboard R/V *Geophizik*, at 21 stations covering the subtidal areas (Table 1, Fig. 1) at depths between 11 and 50 m. Areas <10 m depth could not be surveyed because of navigation difficulties. Sediment structure detail was acquired from Tarasov (1974). At each site a CTD cast was made and mostly four benthos samples were collected with a 0.1 m^2 van Veen grab. The sieved (mesh size 1.0 mm) samples were fixed in 4% formaldehyde solution buffered with sodium tetraborate. In the laboratory, the samples were sieved on 1.0-mm nylon net under running water and transferred to 75% EtOH. All specimens in each sample were identified to the lowest possible taxonomic level, counted and weighed for alcohol wet weight. Molluscs, bryozoans and barnacles were weighed with their exoskeleton.

Calculations

Spatial interpolations of abundance, biomass and approximate production values (see below) were made using the Surfer 7 (Golden Software, Colorado 1999). An estimate of relative production values was used as the parameter in community determinations (Denisenko et al. 2003) and calculated for each species using the following formula:

$$P_s = B_s^{0.75} \times N_s^{0.25}, \tag{1}$$

where P_s approximate production of a species per year or growth season, hereafter referred to as ‘‘relative production’’, B_s biomass (g wet wt m^{-2}), and N_s abundance (ind m^{-2}) of species ‘‘s’’. The equation is based on the relation between production and respiration of a specimen with mass (w_s) as follows: $R = 2.879P$ (Umnov and Alimov 1979), or $P = R_{s1}(w_s^{0.75})/2.879$. For N specimens of a taxon, the total production may be presented as $P_s = R_{s1}(w_s^{0.75})N_s/2.879$. According to Hemmingsen (1960), R_{s1} (average respiration rate of an animal with a mass of 1 g) for most animals is equal to 2.97 KJh^{-1} g^{-1} and that $R_{s1}/2.879$ may be referred to as approximately 1, therefore $P_s = (B_s/N_s)^{0.75}N_s$ (Brey 1990), or $P_s = (B_s)^{0.75}N_s^{0.25}$ (Denisenko and Denisenko 1990). This equation may be considered rough but it is sufficiently accurate and practical for the purpose of community determination.

To calculate the similarity between the samples, the Czekanowski–Soerensen index (Cz) (Czekanowski 1909; Soerensen 1948) was applied. The relative production value of each taxon was used in the calculations as follows:

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

where P_{sa} and P_{sb} are relative production (per m^{-2}) of species ‘‘s’’ at stations ‘‘a’’ and ‘‘b’’, respectively.

Determination of zoobenthic assemblages was made by using a standard hierarchical clustering procedure on data obtained from each sample using the Average Linkage Method (e.g. Pesenko 1982; Pielou 1984) of the ‘‘BioDiversity Pro’’ software (Biodiversity Professional Beta, ©The Natural History Museum & the Scottish Association for Marine Science 1998). Clustering analyses were performed on individual replicates because replicates within a station often showed considerable variability, with one or two replicates from the station belonging to some other community type than the main type observed. Mean ± SD of biomass and abundance values at each station were calculated. Similar calculations between the stations belonging to any specific community type (integrated measure) were made to assess the heterogeneity and patchiness of each community, thus giving insight to the statistical reliability of each measured parameter

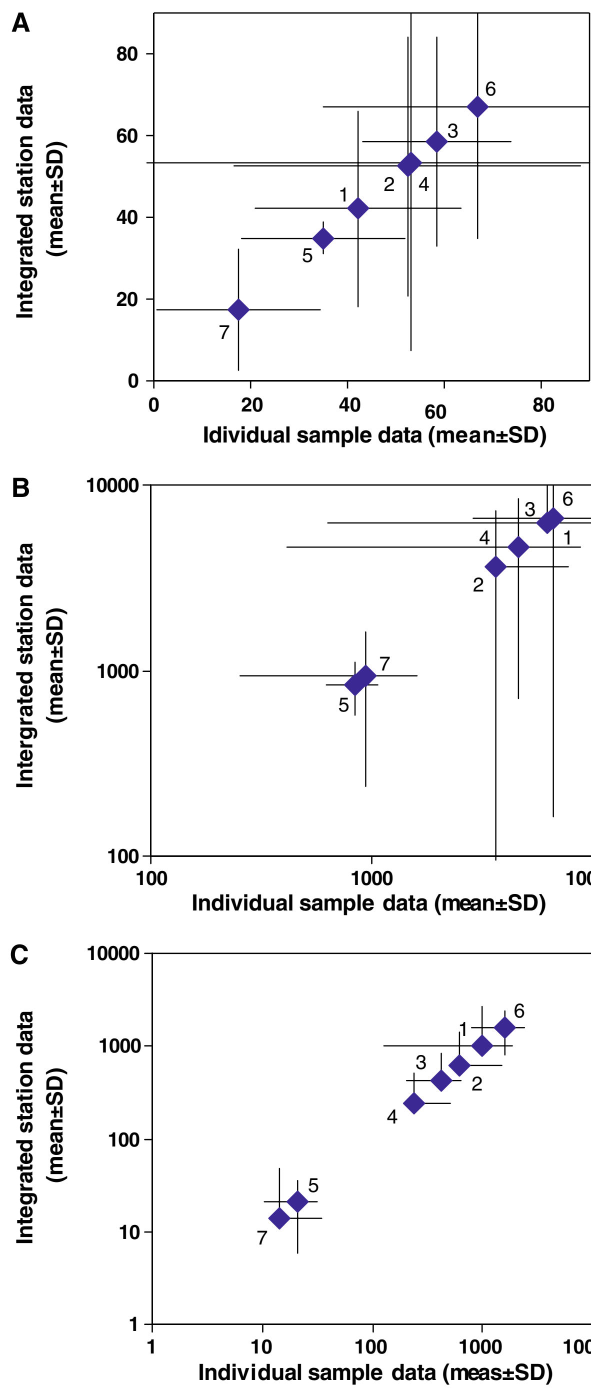

Fig. 2 Variations in **a** the number of species, **b** abundance (ind m^{-2}) and **c** biomass (g m^{-2} gross wet wt) in the different zoobenthic communities in the Cheshskaya Bay. *x*-axis: individual sample data (mean ± SD as horizontal lines); *y*-axis: integrated station data (mean ± SD as vertical lines). The numbering of communities corresponds to the types presented in Table 2

(Fig. 2). Although no clear-cut differences between sample-specific and station-specific data could be found, the latter were considered the more useful method for assemblage mapping.

Species significance in a community was expressed by the ‘‘Species Validity Index’’ (SVI), calculated as the product of relative production and frequency of occurrence (at the stations belonging to a specific community type) of each species (Denisenko et al. 2003). The main feeding mode in each community type was determined by recording the feeding mode of the 15 most dominant species ranked according to the SVI. To examine the relationship between categorical variables graphically, correspondence analysis (CA) was performed. Categories that are similar to each other appear spatially clustered in the graphs, estimated by values of the ‘‘conditional factors’’ 1 and 2 (Clarke and Warwick 2001). The relationships between community distribution and variability in environmental factors were analysed using Classification Tree (CT) (SYSTAT® 9.0, 1998, SPSS, Breiman et al. 1984). All calculations for CA and CT were made using Statistica 6.0 (©StatSoft, Moscow 2001). Diversity was calculated using the Shannon index H' (Magurran 1988) on abundance data of zoobenthos.

Results

Quantitative characteristics and diversity of zoobenthos

In the study area, a total of 419 macrozoobenthic taxa were recorded (Appendix ESM1). The number of taxa at each station varied between 3 and 119 (Fig. 3), with a clear predominance of worms including polychaetes (113 taxa), sipunculids (3), priapulids (1), nemerteans (1) and nematodes (1). Crustaceans (86 taxa), bryozoans (75) and molluscs (72) constituted the next largest systematic groups while organisms from other groups were represented by only a few species.

Total abundance of macrozoobenthic organisms varied between 40 and 290,00 ind m^{-2} with juveniles and up to 4,200 ind m^{-2} without juveniles (Fig. 4). This enormous range arises from the presence of dense populations of barnacles (*Balanus crenatus*; Stations 30, 34, 37, 39 and 43, *Verruca stroemia*; Stations 25 and 26) and mussels (*Mytilus edulis*; Stations 30, 33 and 39, *Modiolus modiolus*; Stations 25, 26, 35, 36 and 44), with many young age classes at some stations. H' (based on abundance) varied between 1.9 and 3.6, indicating marked variability in the structure of zoobenthos in different parts of the bay (Fig. 5). Lower diversity values correspond mostly to stations with single-species dominance, although juvenile stages with body size less than 2 mm were not included in the diversity calculations.

Similar to abundance, biomass also varied considerably, from 0.74 to 6,305 g (with exoskeleton wet wt m^{-2}; Fig. 6a). In the 1930s it had not exceeded 400 g wet wt m^{-2} (Fig. 6b). Molluscs (mainly *M. edulis*) and crustaceans (mainly *B. crenatus*) generally formed the main part of the biomass with the highest values (>6,000 g wet wt m^{-2}) observed in the southwestern part of the bay where these groups predominated. Another high-biomass area occurred in a deeper area close to the entrance of the bay where polychaetes, brachiopods and bryozoans also were well represented. The most abundant populations of hydroids were found southeast of the bay centre. Markedly lower biomass and abundance values of benthic organisms occurred along a wide zone crossing the bay diagonally in northwest–southeast direction.

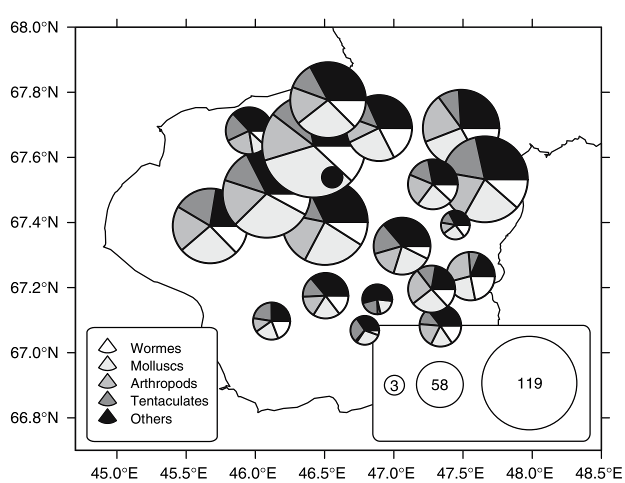

Fig. 3 Numbers and shares of zoobenthic species in the main systematic groups at the Cheshskaya Bay study stations

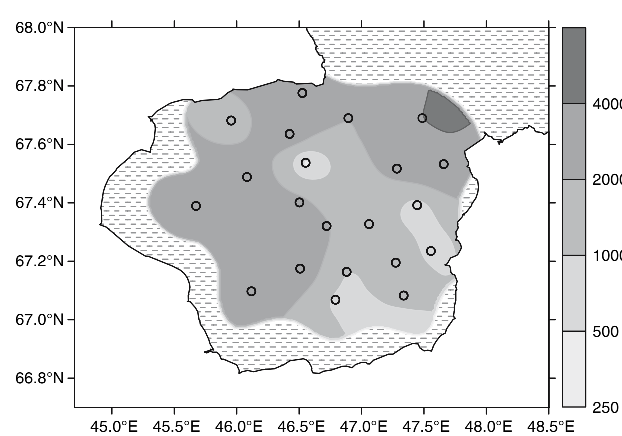

Fig. 4 Abundance distribution (ind m^{-2}) of zoobenthos in the Cheshskaya Bay

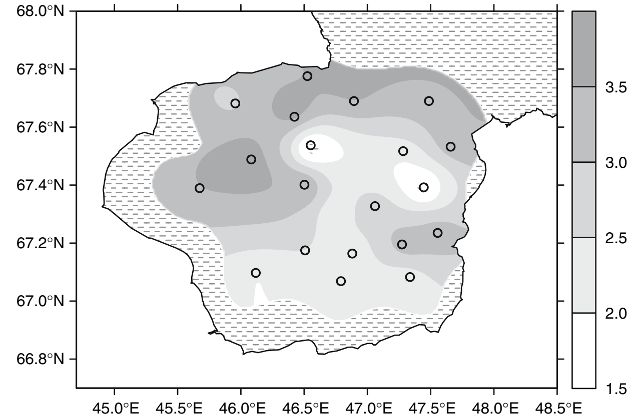

Fig. 5 Shannon diversity index (H') of zoobenthos in the Cheshskaya Bay, based on abundance values

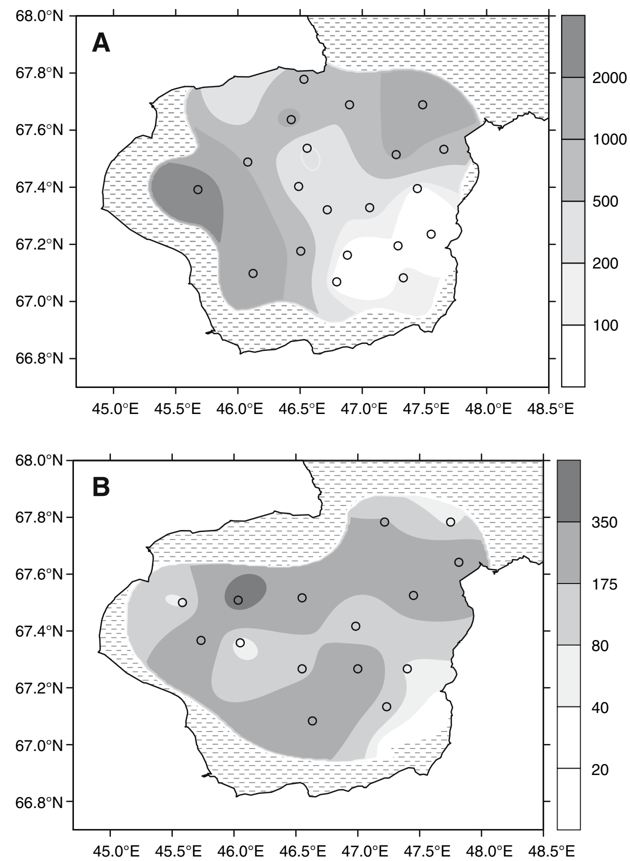

Fig. 6 Total biomass distribution (g wet wt m^{-2}) in the Cheshskaya Bay **a** in 1995 and **b** in 1926, as reconstructed from archive data collected by Brotskaya and Zenkevich (1932)

Community structure

The clustering of relative production values calculated for each sample distinguished seven main benthic community types (Fig. 7). Of the 21 stations investigated, 11 belonged to the two dominating types (Types 1 and 3) and the remaining 10 stations to the other five types (Table 2). Strong dominance (>98%) of suspension feeders (SF) was common for all community types with the exception of Type 7 (Table 3).

Type 1

The *Mytilus edulis–Balanus crenatus*–community type (seven stations, depth range 14–39 m) occurred south of the bay centre on mixed sediments consisting of gravel, pebbles and sand. In this community type the number of species (total 273 taxa, 42 ± 21 per sample), biomass (1007.6 ± 879.6 g wet wt m^{-2}) and abundance (6661 **±** 3799 ind m^{-2}) were high. Although the number of species was high the community was almost completely dominated by only five species with a large number of juveniles.

Type 2

The *Balanus crenatus*–community type (two stations, depth range 28–30 m) was an intermediate type between Types 1 and 3. This type was dominated by barnacles along with *Modiolus modiolus* and *Flustra foliacea* among the five most important species of the total of 207 (53 ± 58 per sample). Biomass (624.3 ± 877.4 g wet wt m^{-2}) and abundance (3620 ± 4093 ind m^{-2}) within this type were less than in Type 1 but higher than in Type 3.

Type 3

The *Modiolus modiolus–Verruca stroemia*–community type (four stations, depth range 27–39 m) was the most

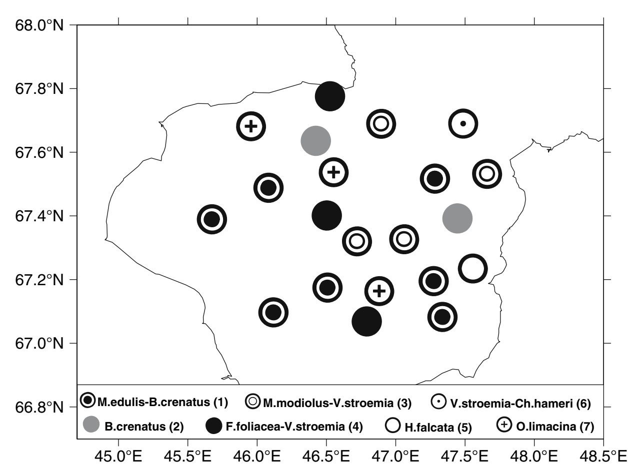

Fig. 7 Distribution of the different zoobenthos communities in the Cheshskaya Bay. The species composition of the different types is shown in Table 2

Table 2 Zoobenthic communities in the Cheshskaya Bay, with five most important species ranked according to the species validity index (SVI, *see text for description*)

Community type (dominant species)	Abundance (ind m^{-2})	Biomass (g wet wt m^{-2})	Frequency of occurrence	SVI
Type 1: *Mytilus edulis–Balanus crenatus*–community (Stations/samples: 7/28. Species in whole community type: 273; species per 0.1 m^{-2}: 42 ± 21; Biomass: 1007.6 ± 879.6 g m^{-2}; Abundance: 6661 ± 3799 ind m^{-2})				
Mytilus edulis	1,179	971.13	0.76	688.6/66.6
Balanus crenatus	3,245	301.09	0.41	220.5/21.3
Balanus sp.	1,507	12.89	0.83	29.6/2.9
Hydroidea g. sp.	51	84.72	0.34	16.7/1.6
Modiolus modiolus	30	285.73	0.10	16.3/1.5
Type 2: *Balanus crenatus*–community (Stations/samples: 2/8. Species in whole community type: 207; species per 0.1 m^{-2}: 53 ± 58; Biomass: 624.3 ± 877.4 g m^{-2}; Abundance: 3620 ± 4093 ind m^{-2})				
Balanus crenatus	2,508	623.87	0.50	435.9/86.0
Flustra foliacea	27	56.53	0.37	13.9/2.7
Modiolus modiolus	10	114.02	0.25	13.1/2.2
Hemithyris psittacea	80	16.81	0.37	9.2/1.8
Didemnum albidum	108	10.19	0.50	8.9/1.5
Type 3: *Modiolus modiolus–Verruca stroemia*–community (Stations/samples: 4/14. Species in whole community type: 255; species per 0.1 m^{-2}: 58 ± 15; Biomass: 418.7 ± 211.9 g m^{-2}; Abundance: 6197 ± 5569 ind m^{-2})				
Modiolus modiolus	48	280.44	0.79	135.7/30.3
Verruca stroemia	5,498	110.64	0.43	124.0/27.9
Didemnum albidum	473	29.63	0.71	41.4/9.2
Balanus crenatus	391	49.92	0.50	40.4/9.0
Flustra foliacea	93	57.10	0.50	31.0/6.9
Type 4: *Flustra foliacea–Verruca stroemia*–community (Stations/samples: 3/12. Species in whole community type: 235; species per 0.1 m^{-2}: 52 ± 35; Biomass: 238.5 ± 264.3 g m^{-2}; Abundance: 4590 ± 4177 ind m^{-2})				
Flustra foliacea	113	177.96	0.75	114.7/41.1
Verruca stroemia	4,019	59.36	0.58	98.8/35.4
Balanus sp.	136	24.82	0.42	12.9/4.6
Modiolus modiolus	43	63.37	0.25	9.1/3.3
Hemithyris psittacea	29	11.91	0.67	9.1/3.3
Type 5: *Hydrallmania falcata*–community (Stations/samples: 1/4. Species in whole community type: 75; species per 0.1 m^{-2}: 35 ± 17; Biomass: 20.95 ± 10.5 g m^{-2}; Abundance: 841 ± 220 ind m^{-2})				
Hydroidea varia	48	7.27	1.00	11.2/38.4
Hydrallmania falcata	10	6.35	1.00	6.7/23.1
Crangon almanni	10	8.00	0.25	2.1/7.2
Hydroidea g. sp.	35	1.42	0.50	1.5/5.2
Escharella immersa	25	0.60	1.00	1.5/4.9
Type 6: *Verruca stroemia–Chirona hameri*–community (Stations/samples: 1/1. Species in whole community type: 67; species per 0.1 m^{-2}: 67 ± 32; Biomass: 1609.4 ± 804.0 g m^{-2}; Abundance: 20635 ± 10300 ind m^{-2})				
Verruca stroemia	14,780	476.00	1.00	1123.6/49.1
Chirona hameri	330	683.20	1.00	569.6/24.9
Balanus balanus	370	177.10	1.00	212.9/9.3
Eucratea loricata	330	83.95	1.00	118.2/5.2
Hiatella arctica	1,900	38.00	1.00	101.0/4.4
Type 7: *Ophelia limacina*–community (Stations/samples: 3/12. Species in whole community type: 96; species per 0.1 m^{-2}: 17 ± 16; Biomass: 14.1 ± 20.4 g m^{-2}; Abundance: 931.6 ± 676.9 ind m^{-2})				
Spongia g. sp.	70	56.00	0.08	4.9/37.0
Ophelia limacina	125	1.40	0.83	2.6/19.7
Spirorbis spirillum	697	1.08	0.25	1.4/10.2
Nephtys longosetosa	20	3.93	0.17	0.9/7.4
Ischinochiton exaratus	95	1.53	0.17	0.7/5.1

Values for species number (per sample and per 0.1 m^{-2}), biomass and abundance (per m^{-2}) in the general description of each community are given as mean ± SD

widespread, occupying the northern and central parts of the bay and characterised by fine and medium grain sized sand with gravel and shell debris. In these areas the number of species was high (total 255 and 58 ± 15 per sample), while biomass (418.7 ± 211.9 g wet wt m^{-2}) was less than half of that recorded for Type 1. The dominance of only a few species was striking in this community type.

Table 3 Feeding types of the most important species in each community type as percentage by biomass (g m^{-2})

Community type	Feeding type			
	SF	DF (SDF/SSDF)	P	G
1: *Mytilus edulis–Balanus crenatus*	99.0	0.0	1.0	0.0
2: *Balanus crenatus*	99.0	0.1	0.9	0.0
3: *Modiolus modiolus–Verruca stroemia*	98.3	1.7 (0.8 / 0.9)	0.0	0.0
4: *Flustra foliacea–Verruca stroemia*	98.1	1.3 (0.0 / 1.3)	0.6	0.0
5: *Hydrallmania falcata*	100.0	0.0	0.0	0.0
6: *Verruca stroemia–Chirona hameri*	100.0	0.0	0.0	0.0
7: *Ophelia limacina*	61.4	30.4 (30.4 / 0.0)	3.2	5.0

The importance of a species in each community type is assessed according to species validity index (see text)

SF feeder, *DF* deposit feeder, *SDF* surface deposit feeder, *SSDF* subsurface deposit feeder, *P* predator, *G* grazer

Types 4, 5 and 6

In the *Flustra foliacea–Verruca stroemia*–community (Type 4, three stations), *Hydrallmania falcata*–community (Type 5, one station) and *Verruca stroemia–Chirona hameri*–community (Type 6, one station), similar trophic structures were observed. The main differences between these types occurred in species composition and some quantitative characteristics. The *F. foliacea–V. stroemia*–community occurred at depths from 14 to 40 m with dominant species similar to those found in Types 2 and 3, but the rest of the community differed markedly. The *V. stroemia–Ch. hameri*–community was found only at the deepest site (Station 25; 49 m) where it exhibited a high biomass (1609.4 ± 804.0 g wet wt m^{-2}) and distinctively low number of species (67 species). The *H. falcata* –community type (one station) showed a characteristically low species richness, abundance and biomass.

Type 7

The *Ophelia limacina*–community type (three stations) was located along the southeast–northwest diagonal of the bay where muddy fine sand was the main sediment fraction. Both the number of species (96 taxa, 17 ± 16) and biomass (14.1 ± 20.4 g wet wt m^{-2}) were comparatively low, and in contrast to the other benthic communities observed in the bay this type comprised a marked portion of deposit feeders (DF) (30.4%).

Effects of environmental factors on the distribution of communities

CA demonstrated the influence of temperature, sediment structure and water depth on the distribution of zoobenthic communities (Fig. 8). However, no clear gradation along the variability in factors could be observed although near-bottom temperature between the stations depended inversely on variability in depth and salinity, and sand content in sediments was opposite to the contents of gravel, clay (pelite) and silt (aleurite).

The CT analysis also showed that near-bottom temperature had a small influence on community distribution, with the low temperature restricting zoobenthic distribution in the deepest part of the bay, namely the *V. stroemia–Ch. hameri* community (Fig. 9). In essence, the major part of the communities varied spatially mainly due to the differences in sediment grain-size than variations in temperature and depth, which, as shown, were interrelated (Fig. 8). The potential influence of differences in near-bottom salinity between the locations was masked by other factors because of small variability (29.5–34.4 PSU).

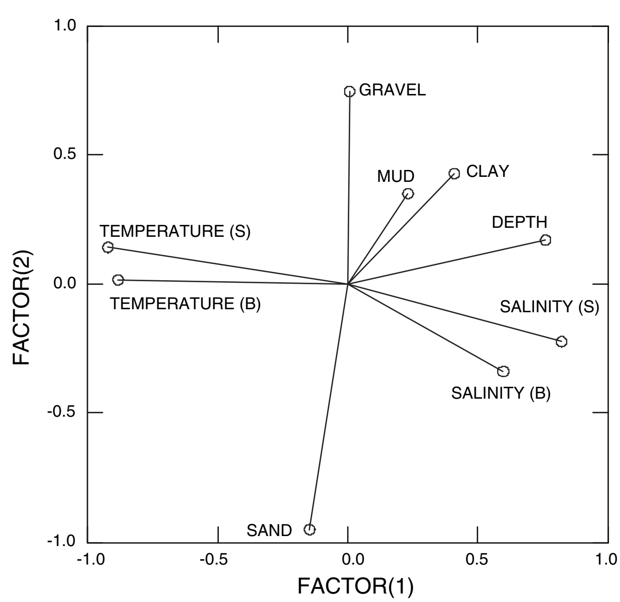

Fig. 8 Results of correspondence analysis (*CA*) of variations in environmental factors in the Cheshskaya Bay. *S* surface, *B* bottom. Factor 1 and Factor 2 are conditional factors, which reflect the gradient of the real interaction of the environmental factors included in the analysis

Discussion

The present study on the macrozoobenthos of the Cheshskaya Bay resulted in 419 taxa, with 16 of them forming dense populations (especially *Mytilus edulis*, *Modiolus modiolus*, *Balanus* spp.), 48 being frequently present in different communities, and the rest having a local distribution or occurring only occasionally. This species richness and composition are more comparable to those from the nearby Onega Bay (White Sea; 521 species; Kudersky 1966), which is characterized by a similar hydrodynamic and temperature regime, than the adjacent open-sea area of the Pechora Sea (712 taxa; Denisenko et al. 2003). In addition, some species, such as the bryozoan *Flustra foliacea*, have not been encountered elsewhere in the Barents Sea while others, such as the bivalve *Modiolus modiolus*, are more often found in the southwestern part of the Barents Sea. Although species richness in the Cheshskaya Bay in general is high, their spatial distribution is not homogeneous despite a relatively consistent oceanographic environment caused by strong water mixing. Also, large variability in species composition within the communities is notable. An uneven distribution in the number of species and the low diversity index ($H' < 2$) in some areas show that the zoobenthos of the Cheshskaya Bay differs from that of other arctic marine bays where anthropogenic stress is also very low (Golikov et al. 1993; Naumov 2001). In areas characterized by unfavourable environmental conditions, a decrease in biodiversity is often observed (Warwick et al. 1987). In the Cheshskaya Bay, anthropogenic stress is considered to be small (Terziev 1992) while the stress caused by physical factors is high especially in the shallow areas characterized by a seasonal temperature range of –1.8 to 14°C, strong tides with erosion effects (1–3 m year^{-1} change during the year due to tectonic processes causing a rising or lowering of land, depending on location, in different areas of the Cheshskaya Bay; Berliant 1986). As such physical factors must be considered the primary cause for the observed low number, abundance and biomass observed in some parts of the bay and strong single-species predominance in other areas.

A clearly lower abundance and biomass, seemingly in conjunction with a low number of species, was found in the southeastern area and in small areas in the centre of the bay. The most likely reason for this is the influence of the southeastern winds and strong tidal currents (Terziev 1992) that transport sediment particles along the bottom, creating unstable habitats. In addition, a freshwater inflow via river discharge that

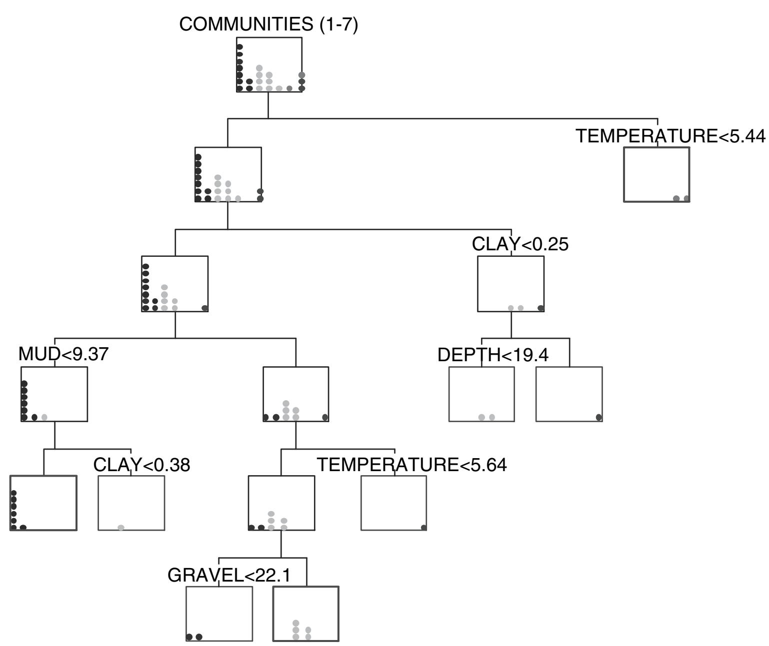

Fig. 9 Classification tree (*CT*) analysis of the distribution of zoobenthos communities along environmental factors (depth, temperature and sediment fractions concentration) in the Cheshskaya Bay. *Each box* containing data is a 'density display' of the community types on a common scale (the same limits and the same direction). When the box occurs on the left side from the split, the relation between a factor and a community type is positive. The number of spots in vertical rows (*lines*) reflects the number of stations contained into a community and the number of vertical lines in the horizontal rows of each box reflects the number of communities related to the examined factors

supplies the area with suspended organic and inorganic matter affects this area (Medvedev and Potechina 1986), although no drastic effect on salinity was recorded in the subtidal areas.

Permanent water mixing, causing high concentrations of fine sand and clay to be constantly present in the near-bottom water layers, regulates larval dispersal, restricts recruitment, and disturbs benthic communities around Oma and Pesha river mouths. In these areas the *Hydrallmania falcata* and *Ophelia limacine*–communities characterised by low species number are found. The *O. limacina* type also occurred at two other stations in the central part of the bay, outside the main stream of the permanent anticyclonic water current, which is characterized by comparatively high concentrations of fine sand in the sediments. In the southwestern part of the bay, outside the soft-bottom zones, abundant numbers of blue mussel and barnacle juveniles were found, as well as a *Mytilus edulis*–community, rich in species and high biomass.

Compared to the rest of the bay, a belt extending across the basin from the southeast to the central part is characterized by lower values for the quantitative zoobenthic characteristics of zoobenthos (Fig. 6a). A similar pattern in zoobenthic biomass distribution in the southeastern part of the bay was obtained using archived data although the general biomass distribution recorded during that time differed somewhat from the present observations (Brotskaya and Zenkevich 1932) (Fig. 6b). The patterns of zoobenthic biomass distribution were similar to minimum nutrient concentrations (Garkavaya and Posdnyakova 1968) and zooplankton biomass (Zelikman 1968) observed along the transect during spring-summer in the 1960s. A lower phytoplankton production in this area, confirmed later by investigations based on satellite data analysis collected over one year (Vinogradov et al. 2000) has also been recorded. All these data indicate that this part of the Cheshskaya Bay is characterized by a lower trophic status most likely caused by the influence of river- and estuarine-originated suspended matter entering the bay (Medvedev and Potechina 1986). Also the transparency of water masses within the area is lower in comparison to the rest of the bay (Garkavaya and Posdnyakova 1968; Pushkin 1968; personal observations). Moreover, a similar decrease in zoobenthic biomass has been observed in the Ob and Yenisey Bays (Kara Sea) in areas influenced by substantial inputs of suspended matter associated with the high freshwater discharge (Denisenko et al. 1999). Outside the area characterized by a high concentration of mineral particles in the water column, high amounts of suspended organic carbon entering from of Pesha and Oma estuaries and numerous small rivers accompanied by estuary-originated phytoplankton as well as under-ice phytoplankton (usually rich in areas of floating ice; Smith 1987) apparently increase zoobenthic biomass. Besides the ample food sources, the presence of suitable substrata, and the successful settlement and development of juvenile sessile suspension feeders has lead to the formation of bottom communities rich in species in this area (Table 2). In contrast to the general zoobenthic feeding pattern in the study region, the deposit-feeding mode was notably common in *Ophelia limacina*–community. Taking into account all characteristics of zoobenthos studied here (species number, diversity, abundance and biomass values) the *Ophelia limacina*–community can be regarded as a stressed community.

The structure and distribution of the communities described in the present paper cannot easily be compared with earlier studies whose investigations were based on of species biomass estimation (Brotskaya and Zenkevich 1932; Pushkin 1968). Furthermore, methodological dissimilarities in sampling procedures and differences in the station network complicate comparability. Still, the communities described here should be regarded as true communities. According to published data, the *Modiolus modiolus*–community is found near the Kola Peninsula coast in the Barents Sea (Zatsepin 1962) and in the Onega Bay in the White Sea (Golikov et al. 1985). The *Mytilus edulis* community is widely spread in the intertidal zone in the whole Northern Hemisphere, and also in Russian Arctic seas, sometimes inhabiting sublittoral rocky bottoms of straits such as the Gorlo Strait in the White Sea (Denisenko et al. 2006) and the Yugorskiy Shar Strait in the Barents Sea (Denisenko et al. 2003). Its presence in the sublittoral zone of bays with normal marine salinity range is not usual because of strong predatory pressure mainly by starfishes (Scarlato 1995). Earlier, *Hydrallmania falcata* and *Balanus crenatus*–communities have been observed in the Gorlo Strait (Denisenko et al. 2006) and an *Ophelia limacina* -community in the Pechora Sea (Denisenko et al. 2003), the first-mentioned community on sandy bottom, the second on rocks and boulders and the last in soft mixed sediments. The *Verruca stroemia–Chirona hameri*–community should be regarded as a separate community because its species composition differs markedly from the other communities. Moreover, in addition to the Cheshskaya Bay *Ch. hameri* is found only in two other regions of the Barents and White Sea areas, namely in the Kara Gate and the Voronka Straits (Rjepishevskiy, 1968), both characterized by high-speed currents. The *F. foliacea–V. stroemia*–community can be regarded as a transitional community between the *M. modiolus–V. stroemia*–community and the *B. crenatus*–community, but in an earlier study performed in the White Sea using scuba diving the latter was described as a separate community (Golikov et al. 1985).

All the studies carried out in the Cheshskaya Bay support the view of the predominance of sessile suspension feeders in the sublittoral zone of the bay. Furthermore, the bottom fauna of the bay differs from many other bays in the region that are characterized by the presence of a sill between the bay basin and the open sea area (Golikov et al. 1993; Denisenko et al. 1999).

Conclusions

Abundant food sources and favourable environmental factors (greatly elevated temperature, no strong geographical variations in temperature, normal marine salinity range and distribution patterns of suspended matter) during the growing season support the specific features (predominance of suspension feeding mode and high abundance and biomass) of the bottom fauna of the Cheshskaya Bay in the sublittoral zone below 10 m depth. These factors promote the occurrence of Atlantic endemic species, which are not found in other parts of the southeastern Barents Sea. The area's zoobenthos is mostly characterized by high abundance and biomass, with molluscs and crustaceans dominating. A decrease in species number, abundance and biomass as well as diversity is observed along a gradient in sediment structure from mixed sediments with pebbles to fine sediments with a dominance of mud and clay. High diversity indices and rich communities imply an unstressed zoobenthic community in most parts of the bay. Nevertheless, the distribution of species in the area is not homogeneous and is regulated by their tolerance to the variability in local environmental conditions. A species-rich zoobenthos dominated by suspension feeders inhabits the majority of the study area while deposit feeders appear in areas characterised by uncomfortable environments.

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