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MARINE BIOLOGY

Phytoplankton in the Northwestern Kara Sea

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Abstract—Studies were conducted in the northwestern Kara Sea in late September of 2007 and 2011. The assessment of species, size, structure, abundance, and biomass of phytoplankton and the role of autotrophic and heterotrophic components in phytocenoses was conducted. The abundance of autotrophic micro-, nano- and picoplankton increased by more than an order of magnitude in each of the following smaller-sized groups of algae. Microphytoplankton dominated in the total biomass of autotrophic phytoplankton. The wet biomass of microphytoplankton was 2.5 times higher than the wet biomass of nanophytoplankton and 5 times higher than that of picoplankton. Nanophytoplankton dominated in abundance and biomass in the heterotrophic component of phytoplankton. The ratio of the total abundance of autotrophic and heterotrophic phytotoplankton was 7 : 1, the ratio of the wet biomass of the both groups was 2.5 : 1, and the proportion of the carbon biomass was 2 : 1. Three biotopes were distinguished in the area of the outer shelf, the continental slope, and the deepwater area adjacent to the St. Anna Trough, which differed in composition and quantitative characteristics of phytocenoses. Frontal zones dividing the biotopes are characterized by high phytoplankton biomass and the dominance of diatoms in the community (more than 40% of the total biomass), which indicates the local availability of "new" nutrients for planktonic algae.

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INTRODUCTION

The northwestern part of the Kara Sea is the most complex region of the basin. This is the region of interaction between the waters of the Kara Sea shelf and the Central Arctic. The flow of the warmer and more saline waters of Atlantic origin which propagate from the northwest along the western part of the St. Anna Trough and the eastern Novaya Zemlya current flowing to the northeast along the Kara Sea coast of the Novaya Zemlya have a considerable effect on the hydrobiological structure and water dynamics in the region [2, 15]. The northern boundary of the surface lens of waters desalinated by the freshwater runoff of the Ob and Yenisei rivers lies in the northwestern part of the Kara Sea [1, 2]. The interaction of the waters of different origin forms the system of distinct frontal zones in the region. The northwestern part of the basin is characterized by a high diversity of environmental conditions in which the planktonic community functions. Up to the present, the features of the arctic phytocenosis formed under such conditions were unknown.

The aim of this study is to assess the qualitative composition, abundance, size structure, biomass of pelagic algae, and the contribution of autotrophic and heterotrophic components of phytoplankton to the qualitative characteristics in the northwestern Kara Sea. The features of the phytocenosis structure were analyzed in relation to the hydrophysical and hydrochemical conditions of particular areas–biotopes.

AREA OF STUDY, MATERIALS AND METHODS

The samples were collected during two cruises aboard the RV *Academician Mstislav Keldysh* on September 23–25, 2007 and September 28–29, 2011. The studies were conducted in the outer shelf from depths of 115–140 m, in the region of the continental slope and in the St. Anna Trough with depths of 545–555 m. In 2007, 52 phytoplankton samples were collected at 9 stations along the quasimeridional transect in the latitude range from 75°33.3′ to 76°55.5′ N; in 2011, a total of 32 phytoplankton samples were collected at 8 stations along the transect between 76°17.0′ and 76°58.4′ N (Fig. 1).

Samples for phytoplankton analysis were taken from 5- to 3-L Rosette Niskin bottles. The sampling depths were selected after the initial CTD profiling of the vertical distribution of temperature, salinity, and chlorophyll fluorescence. Samples were collected from four to six layers, which covered the upper mixed layer (2–3 samples), the pycnocline and/or the layer of the fluorescence maximum (1–2 samples), and the layer below the pycnocline (1–2 samples).

The phytoplankton was concentrated by a gentle reverse filtration technique using Lavsan filters with a

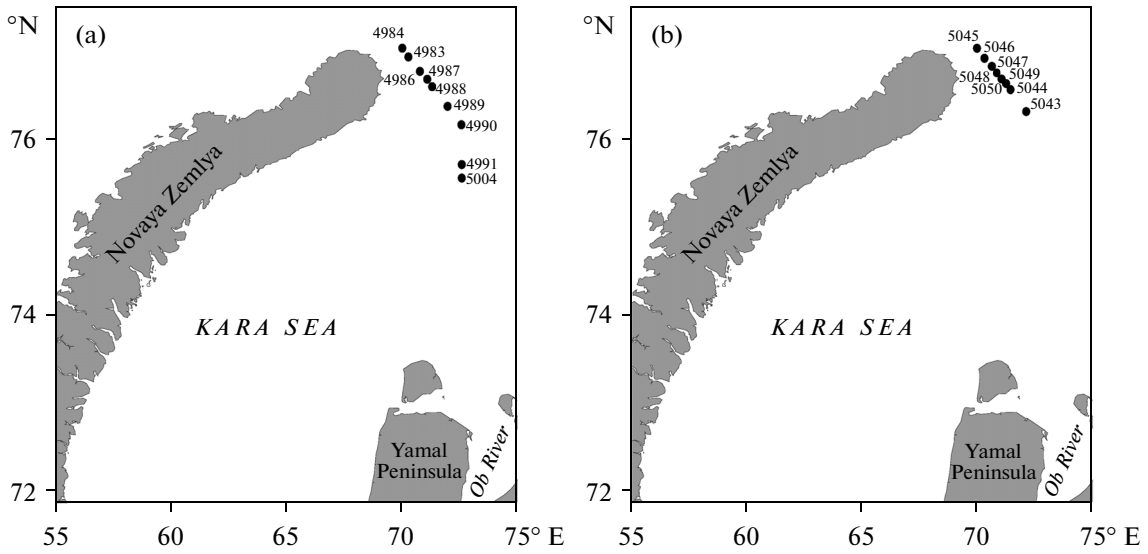

Fig. 1. Scheme of stations in 2007 (a) and in 2011 (b).

pore diameter of 1 μm. The technique was developed at the Institute of Oceanology [7]. Most samples were processed without fixation in a living state immediately after concentration or within one or two days after the sampling. The live samples were stored in a refrigerator at a temperature of 2–3°C. The samples were assessed in a Nojeotte counting chamber (with a volume of 0.084 mL, 400 × magnification) and a Naumann chamber (with a volume of 1 mL, 200 × magnification) using Jena Lumar, Leica, and Biolam 2 var. 12. Phytoplankton samples were examined under light and fluorescent regimes to detect heterotrophic forms. After processing the live material, all samples were fixed in 1% solution of neutral formalin to estimate the abundance of large forms of diatoms and dinoflagellates under stationary conditions. The wet-cell biomass was calculated based on the principle of the geometric similarity using the data from measurements of their linear dimensions and volumes. The carbon content in the cells was calculated using appropriate coefficients for different taxonomic and size groups [14, 16, V.I. Vedernikov unpublished data].

The data on picophytoplankton (cell diameter of 1–2 μm) and the smallest forms of nanoplankton (diameter of 3–6 μm) were obtained using samples collected in 2011. For enumeration of pico- and nanoplankton, water samples were taken from the same bottles and from the same layers as the phytoplankton samples. Samples for pico- and nanoplankton quantification were prepared by staining 50 mL of water with primulin, preserved in 3.6% glutaraldehyde solution and filtered through black nuclear membranes with a pore size of 0.4 μm [9, 12, 13] using our modification of technique [17]. Then the samples were immediately frozen and stored at –24°Cuntil analysis under stationary conditions using a Leica DM 5000 luminescent microscope at the magnification ×200–1000. Small and numerous forms were counted in 50–100 microscope fields of view; rare forms were counted by the total examination.

Cell volumes were calculated on the basis of their size and the principle of similarity to appropriate stereometric figures. The organic carbon content of algae was estimated from their cell volumes [14].

RESULTS

Species structure and a heterotrophic component of the phytocene. The materials characterized the autumn stage of phytocene succession. In the surveyed area, 166 species of algae were detected in phytoplankton and 12 forms were identified by genus. Dinophyceae (81 specie) and (Bacillariophyceae (54 species) had the largest number of species. The other classes had less species diversity: Cryptophyceae (8 species), Prymnesiophyceae (7 species), Prasinophyceae (4 species), Chrysophyceae (4 species), Dictyochophyceae (3 species), Euglenophyceae (1 pecies), Pedinophyceae (1 species), Ebriidea (1 species), Choanoflagellidae (1 species), and Siluaniacea (1 species).

Most species were detected in the samples during both years of studies. The frequency of occurrence of 47 species was more than 80% (according to the number of stations); 63 species of algae typical for the Kara Sea were recorded only during one year of studies. They were, mainly, species recorded at 1–2 stations, rarely at 3–4 stations and not numerous. Thus, in 2007, the most frequent species were *Chaetoceros diadema* (occurrence at 89% of stations, maximum abundance 18.0×10^6 cells/m^2), *C. concavicornis* (55%,

6.0×10^6 cells/m^2), *C. debilis* (55%, 10.2×10^6 cells/m^2), *C. decipiens* (55%, 6.0×10^6 cells/m^2), *Eucampia graenlandica* (77%, 47.2×10^6 cells/m^2), and *Paralia sulcata* (55%, 3.2×10^6 cells/m^2). In 2011, only one species of diatoms, *Chaetoceros tenuissimus*, was numerous and frequent. The species was recorded at 87% of stations and reached the maximum abundance (7.8×10^6 cells/m^2). Among Dinophyceae, 17 species were recorded in 2007 and 19 species in 2011. Most of these species had extremely low abundance and were detected at 1–2 stations. Only three species of Dinophyta, *Torodinium teredo*, *Alexandrium ostenfeldii*, and *Protoperidinium granii* reached the maximum abundance 0.41×10^6, 0.39×10^6, and 0.26×10^6 cells/m^2, respectively and were detected at 50% of stations in 2011.

In 2011, the taxonomic list was added to with 11 autotrophic and 2 heterotrophic species of pico- and nanoplankton algae. Their identification became possible due to fluorescence microscopy. In this list, 7 autotrophic species were abundant and determined the quantitative characteristics of the phytoplankton. The abundance (>95%) and biomass (>90%) of picoplankton at all stations were formed by *Micromonas pusilla* (the cell diameter of 1.5 μm), a representative of the class Prasinophyceae. The maximum abundance of the species in the surface layer at station 5043 reached 35×10^6 cells/L. One more species of picophytoplankton, *Resultor micron* (Pedinophyceae) was found only at the northern stations of the transect (to the north from station 5048, Fig. 1) with the maximum abundance 0.7×10^6 cells/L at station 5046. Among nanoplanktonic autotrophic algae (cell diameter from 3 to 10 μm), 5 species, namely *Plagioselmis prolonga*, *Hemiselmis anomala* (Cryptophyceae), *Pyramimonas grossi* (Prasinophyceae), *Imantonia rotunda*, and *Dicrateria* sp. 1 (Prymnesiophyceae) had high abundance. The two latter species, as well as *R. micron*, were found only at the northern stations of the transect (Table 1, Fig. 2). *Plagioselmis prolonga* and *Hemiselmis anomala* reached their high abundance in the middle and southern parts of the surveyed area. The five above-mentioned species of nanoplankton constituted from 23.5 to 64% of the total abundance of the autotrophic phytoplankton and from 6.3 to 48.2% of the total carbon biomass. Four autotrophic species of nanophytoplankton, *Apedinella spinifera*, *Karlodinium venificum*, *Pyramimonas octopus*, and *Rhodomonas* sp., and one heterotrophic species, *Caecitellus parvulus*, were recorded only at one station and were not abundant. The heterotrophic species *Telonema subtilis* had also low abundance but was recorded at all stations.

In samples collected in 2011, heterotrophic forms constituted from 7 to 20% of the total abundance of phytoplankton (on average 13.7% along the transect) and from 23 to 42% of the total wet biomass (on average ~30% along the transect). The species identification of heterotrophic forms was made, mainly, in the size group with cell diameter >10 μm (cell volume

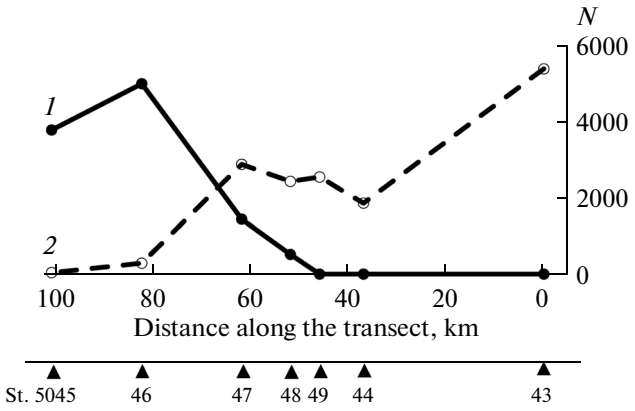

Fig. 2. Distribution of the total abundance ($N \times 10^6$ cells/m^2) of phytoplankton species typical for northern (*1*) and southern (*2*) regions of the surveyed area in the Kara Sea. 2011. The 0–25 m layer. *1*, *Imantonia rotundata*, *Dicrateria* sp. *2*, *Hemiselmis anomala*, *Plagioselmis prolonga*.

>500 μm^3 (Table 2, Fig. 3). In this size group, 15 species of the genus Protoperidinium (*P. bipes*, *P. brevipes*, *P. brochi*, *P. cerasus*, *P. depressum*, *P. divergens*, *P. globulus*, *P. granii*, *P. okamurai*, *P. pallidum*, *P. pellucidum*, *P. pyriforme*, *P. roseum*, *P. steinii*, and *P. subinerme*), 3 species of the genus Gyrodinium (*G. spirale*, *G. fusiforme*, and *G. lachrymal*), 4 species of the genus Gymnodinium (*G. blux*, *G. albulum*, *G. stellatum*, and *G. heterostriatum*), 3 species of the genus Cochlodinium (*C. citron*, *C. helicoides*, and *C. Archimedes*), 2 species of the genus Warnowia (*W. makulata* and *W. schuettii*) and *Amphidinium sphaenoides*, *A. longum*, *Katodinium glaucum*, *Actiniscus pentasterias*, and *Pronoctiluca pelagica* were identified. Among nanoplanktonic forms (cell diameter from 3 to 10 μm), *Gyrodinium* sp. 1, which formed from 2 to 17% of the total abundance of heterotrophs, was identified to the genus. *Telonema subtilis*, *Leucocryptos marina*, and *Monosiga marina* were identified to the species. Their contribution to the total abundance of heterotrophic forms did not exceed 3–5%.

The size structure of the phytocene according to data from 2011. The analysis of the size structure of autotrophic phytoplankton has demonstrated that picophytoplankton dominates by the number of cells (88–93% of the total abundance of autotrophic phytoplankton) at the end of the vegetation period (Tables 1, 2). Nanophytoplankton (cell volume is 5–500 μm^3) formed 5.5–10.4%, and microphytoplankton formed not more than 1.5% of the total number of cells. In most cases, microphytoplankton dominated in the wet biomass of the phytocene including picophytoplankton constituting from 47.2 to 81.3% of the total wet biomass of algae (Fig. 4a), except stations 5043 and 5046. The contribution of the three size groups to the total wet biomass of phytoplankton was almost equal at station 5043, and picoplankton was the dominant

Table 1. Abundance ($N \times 10^6$ cells/m^2), abundance of picophytoplankton ($N \times 10^9$ cells/m^2), wet biomass (B_w, mg/m^2), carbon biomass (B_c, mg/m^2) of phytoplankton in the layer of 0–25 m in the northwestern Kara Sea in 2011 (September 28–29, 2011)

No. of stations	Parameters	Bacillariophyceae	Dinophyceae	Prymnesiophyceae			Cryptophyceae	Prasinophyceae	Euglenophyceae	Other identified	Unidentified >5 μm	Unidentified >5 μm	Total	Picophytoplankton
				Coccolithales	Imantonia, Dicrateria	Phaeocystis								
5043	N	23.6	95.6	11.8	–	830.8	**5396.5**	1234.9	23.9	7.0	195.8	**4898.7**	13019.2	**217.8**
	B_w	22.78	343.0	6.74	—	25.74	**158.66**	25.64	13.83	19.42	54.83	103.89	775.15	**422.2**
	B_c	2.53	34.46	0.99				4.59	2.07	2.14	8.28	18.37	106.53	**83.1**
5044	N	**1006.7**	270.3	24.3	–	**2935.0**	1862.0	321.5	79.5	15.0	294.1	2484.7	9293.1	97.6
	B_w	**1157.1**	**1379.0**	8.48	—	**77.43**	111.76	5.71	46.12	15.55	142.8	103.03	**3046.99**	175.8
	B_c	**111.18**	**127.86**	1.21	—	**12.78**	19.29	1.0	6.92	1.78	21.09	17.34	**320.45**	36.7
5049	N	111.5	**336.9**	**64.7**	–	1719.0	2547.5	726.5	**121.0**	1.3	136.0	2761.3	8525.7	137.1
	B_w	111.6	926.12	**19.83**	—	29.97	153.6	19.61	**70.2**	4.2	57.26	69.68	1462.1	246.6
	B_c	15.47	87.17	**2.98**	—	5.4	31.7	3.45	**10.49**	0.44	8.53	12.15	177.78	51.3
5048	N	**993.6**	164.6	6.2	517.3	942.5	2433.0	465.8	48.0	7.3	81.75	2869.9	8530.0	108.4
	B_w	**1017.06**	975.5	14.63	57.58	16.49	114.94	12.21	27.83	4.64	21.91	78.0	2340.79	196.5
	B_c	**117.37**	81.29	1.71	9.9	2.98	25.64	2.13	4.23	0.53	3.36	13.53	262.67	40.8
5047	N	400.0	217.0	10.85	1440.8	1237.8	2881.8	177.4	83.9	**35.28**	232.8	1849.8	8567.4	135.9
	B_w	533.78	523.85	5.63	104.24	22.41	129.8	18.5	48.6	**27.73**	97.12	62.55	1574.2	244.1
	B_c	66.57	49.59	0.85	16.72	4.01	22.41	2.89	7.26	**3.19**	14.48	10.74	198.71	50.8
5046	N	19.8	138.8	6.7	**5005.5**	1877.0	286.8	1290.3	0.1	0.1	**924.7**	3944.0	**13493.8**	115.0
	B_w	63.04	442.26	8.25	**423.98**	37.1	18.3	24.91	0.06	0.6	**400.4**	**172.72**	1591.61	206.5
	B_c	8.54	41.17	1.23	**74.94**	6.25	3.95	4.47	0.01	0.07	**59.57**	**29.09**	229.29	43.9
5045	N	163.3	84.1	5.6	3786.0	2366.0	39.5	**2186.8**	5.5	0.5	108.8	652.8	9398.9	110.0
	B_w	247.99	442.0	4.78	370.6	12.63	3.78	**28.5**	0.94	2.13	56.9	28.4	1198.63	206.5
	B_c	16.24	37.6	0.7	59.95	2.73	0.68	**5.22**	0.06	0.24	8.39	4.77	136.58	46.3

The maximal values are in bold type.

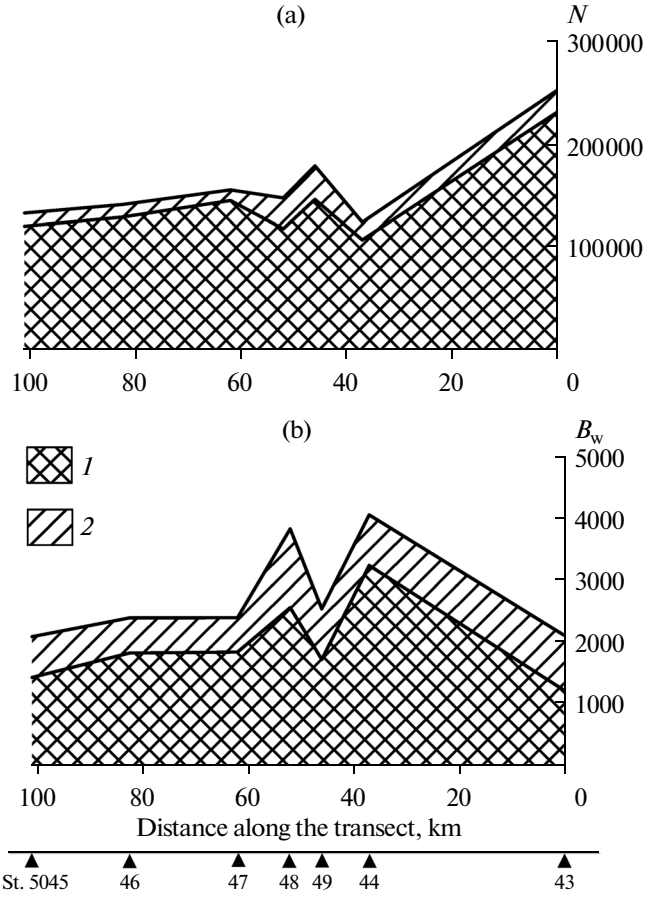

Fig. 3. Ratio of the abundance, $N \times 10^6$ cells/m^2 (a) and wet biomass, B_w mg/m^2 (b) of autotrophic (*1*) and heterotrophic (*2*) phytoplankton in the 0–25 m layer, 2011.

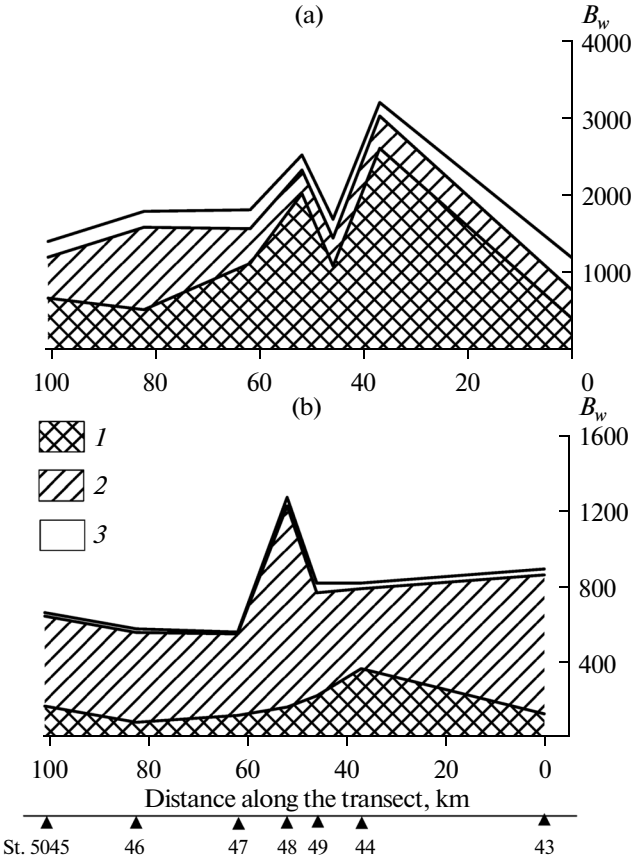

Fig. 4. Ratio of the wet biomass (B_w, mg/m^2) of different size groups of autotrophic (a) and heterotrophic (b) phytoplankton in the 0–25 m layer, 2011. *1*, microphytoplankton; *2*, nanophytoplankton; *3*, picophytoplankton.

group (43.8%) according to carbon biomass, determined by the high carbon content in cells of picoalgae. At station 5046 the wet biomass was mainly formed by nanophytoplankton (53.4%) due to the high abundance of two species of small-sized algae *Imantonia rotunda* and *Dicrateria* sp. 1 (200.2 × 10^3 cells/L). Nanophytoplankton dominated in carbon units, not only at station 5046 (64.3%) but at station 5045 (49.0%) as well, where *Imantonia rotunda* and *Dicrateria* sp. 1 were also abundant. Microphytoplankton dominated in the carbon biomass at other stations of the transect (Table 2).

Nanophytoplankton prevailed in the heterotrophic component of the phytocene and constituted from 43 to 75% of the total abundance of this group of algae. Nanoplankton formed 52.2–84.3% of the total wet biomass of heterotrophic phytoplankton and 47.0–87.4% of the carbon biomass (Fig. 4b, Table 2).

The characteristic feature of the phytocenosis is the ratio of autotrophic and heterotrophic forms in each of three size groups (Table 2). The portion of heterotrophs in the total abundance of picoplankton was low at all stations and constituted from 1.8 to 11.8%. The portion of the heterotrophic component in the wet and carbon biomass of picoplankton varied from 3.3 to 19.0%.

The portion of heterotrophic algae in nanophytoplankton (cell diameter of 3 to 10 μm) differed considerably at different stations of the transect. At stations 5044, 5045, and 5047, the contribution of autotrophic and heterotrophic nanoplankton to abundance and biomass were similar. At station 5043, where the abundance of auto- and heterotrophic algae was similar, the wet biomass and carbon biomass of heterotrophic forms was much higher and constituted 67 and 63%, respectively. This can be explained by the dominance of small cells of average volume ~30 μm^3 in autotrophic nanoplankton, whereas the average volume of heterotrophic nanoplankton was twice as high. At stations 5048 and 5049, the portion of heterotrophs in nanophytoplankton abundance increased to 68.2 and 63.5%, respectively. At the same stations the portion of heterotrophs in wet and carbon biomasses of nanoplankton was 77.6 and 74.3%, respectively (sta-

Table 2. The contribution of three size groups of autotrophic (A) and heterotrophic (H) phytoplankton to abundance ($N \times 10^6$ cells/m^2), wet biomass (B_w, mg/m^2), and carbon biomass (B_c, mg/m^2) in the layer of 0–25 m (September 28–29, 2011). V, cell volume, μm^3. D, the diameter of spherical cells, μ

No. of stations	Group	N			B_w			B_c		
		$V > 500$ $D > 10$	$V - 10–500$ $D - 3–10$	$V < 10$ $D < 2.5$	$V > 500$ $D > 10$	$V - 10–500$ $D - 3–10$	$V < 10$ $D < 2.5$	$V > 500$ $D < 10$	$V - 10–500$ $D - 3–10$	$V < 10$ $D < 2.5$
5043	A	153.0	12833.6	**217817.2**	404.6	370.6	**422.2**	42.27	64.26	**83.1**
	H	61.6	12466.2	8944.2	118.7	742.6	32.4	10.29	109.78	6.48
5944	A	**1360.7**	7932.7	97640.8	**2622.9**	424.1	175.8	**247.85**	72.26	36.7
	H	**234.9**	8562.7	8237.0	**361.44**	427.1	29.6	**36.68**	37.55	5.89
5049	A	522.5	8003.2	137121.0	1083.5	366.1	246.6	108.82	68.96	51.34
	H	130.6	13933.6	**18440.4**	215.1	551.6	**51.0**	21.68	91.46	**10.3**
5048	A	1200.6	7329.4	108385.9	2031.1	309.8	196.5	203.85	58.82	40.85
	H	65.0	**15687.4**	14202.6	154.9	**1076.3**	46.2	15.81	**173.48**	9.25
5047	A	694.2	7873.2	135900.3	1120.4	453.8	244.1	128.62	70.44	50.8
	H	126.1	7617.5	2448.0	110.5	435.5	8.6	15.48	70.65	1.71
5046	A	164.9	**13328.9**	114986.6	514.1	**1077.6**	206.5	53.7	**175.59**	43.86
	H	59.6	5633.4	6392.3	74.3	479.8	19.9	9.74	80.72	3.98
5045	A	245.9	9153.0	110054.7	662.6	536.0	206.5	47.04	89.54	46.3
	H	114.0	7629.6	5059.2	160.0	482.2	18.3	25.06	89.59	3.64

The maximal values are in bold type.

tion 5048) and 60 and 57% (station 5049). The dominance of autotrophic nanophytoplankton by abundance, wet biomass, and carbon biomass was found only at station 5046, which is caused by the mass growth of two species of the genus Prymnesiophyceae.

Autotrophic algae dominated by abundance, wet biomass, and carbon biomass in the microphytoplankton size group at all stations (Table 2, Fig. 3).

Phytoplankton abundance, 2011. In the autotrophic component of the phytocene the abundance of picoplankton was an order greater than the abundance of both nano- and microphytoplankton and ranged within 97.6–217.8 × 10^9 cells/m^2 (3.9–8.7 × 10^6 cells/L) (Table 1). *Micromonas pusilla* constituted more than 95% of the abundance of picoalgae. At all stations the abundance of heterotrophic picoplankton was lower than the abundance of autrotrophic picoplankton more than by an order of magnitude and ranged within 2.4–18.4 × 10^9 cell/m^2 (1.0–7.4 × 10^5 cells/L). At some stations (5043, 5045, and 5047) the abundances of auto- and heterotrophic picoplankton differed by a factor of 20–50 (Table 2).

The abundance of autotrophic nanophytoplankton in the surveyed area varied in a small range from 7.9 × 10^9 to 13.3 × 10^9 cells/m^2 (3.0–5.3 × 10^5 cells/L). Maximum abundance was recorded at stations 5043 and 5046 (Table 2). Two small-sized species of Cryptophyceae, *Plagioselmis prolonga*, and *Hemiselmis anomala*, with an average cell volume ~35 μm^3 dominated at station 5043, where they formed 42% of the abundance of autotrophic nanophytoplankton (the total abundance of the two species was 2.2 × 10^5 cells/L). At station 5046, the species *Imantonia rotunda* and *Dicrateria* sp. 1 with an average cell volume ~85 μm^3 formed 37.6% (2.0 × 10^5 cell/L) of the abundance of nanophytoplankton. The high abundance of unidentified cells of nanophytoplankton with a diameter of 3–5 μm was recorded at these two stations (Table 1). Unidentified cells comprised 37.6% and 29.2% of autrophic nanophytoplankton at stations 5043 and 5046, respectively.

The maximum abundance of heterotrophic nanoplankton 12.5–15.7 × 10^9 cells/m^2 (5.0–6.5 × 10^5 cells/L) was recorded at stations 5043, 5048, and 5049. In other parts of the surveyed area the number of cells of this group varied in the small range 5.6–8.6 × 10^9 cells/m^2 (2.3–3.4 × 10^5 cells/L).

The abundance of autotrophic and heterotrophic microphytoplankton was low at all stations and ranged from 0.1 to 1.4%, respectively, of the total abundance of algae in each of these groups. The maximum abundances of autotrophic microphytoplankton 97.6–1.4 × 10^9 cell/m^2 and 1.2 × 10^9 cell/m^2 (54.4 × 10^3 and 48.0 × 10^3 cells/L, respectively) were recorded at stations 5044

Table 3. Abundance ($N \times 10^6$ cells/m^2), wet biomass (B_w, mg/m^2), carbon biomass (B_c, mg C/m^2) of phytoplankton in the 0–25 m layer (September 23–25, 2007)

No. of stations	Characteristics	Bacillariophyceae	Dinophyceae	Prymnesiophyceae	Chrysophyceae	Unidentified >5 μm	Other identified	Flagellatae >5 μm	Total	Flagellatae <5 μm*
4984	N	160.14	288.67	62.94	20.3	676.08	51.18	456.85	1716.16	877.51
	B_w	754.44	972.48	18.99	1.02	42.29	74.36	63.14	1863.58	28.76
	B_c	34.49	87.23	2.85	0.15	8.49	9.70	10.18	153.09	4.34
4983	N	52.31	239.25	51.68	9.74	413.54	16.14	640.9	1423.56	1114.9
	B_w	131.48	457.39	13.26	0.49	104.76	17.47	134.07	724.85	48.38
	B_c	6.34	52.86	2.01	0.07	20.95	2.60	20.20	105.03	8.05
4986	N	113.13	155.49	73.12	3.8	323.82	55.45	568.47	1293.28	809.81
	B_w	195.12	687.43	14.89	0.19	55.05	44.31	82.22	1079.21	23.07
	B_c	30.80	61.84	3.06	0.03	11.31	10.02	13.47	130.53	3.46
4987	N	209.84	225.13	274.47	125.43	479.04	79.58	1199.62	2593.11	2880.37
	B_w	345.96	657.97	59.42	6.40	81.40	31.54	185.74	1368.43	115.21
	B_c	19.27	60.51	8.91	0.96	16.29	4.60	27.86	138.40	19.2
4988	N	36.17	139.15	81.76	29.65	70.0	19.47	679.37	1055.57	1029.45
	B_w	48.57	795.14	17.69	1.71	11.9	42.07	73.97	991.05	32.84
	B_c	4.02	63.43	2.65	0.26	2.4	5.21	11.1	89.07	5.2
4989	N	177.53	193.95	78.87	25.02	96.3	3.4	412.29	987.36	1352.13
	B_w	108.93	443.02	10.0	1.25	11.63	2.02	34.91	611.76	50.64
	B_c	11.27	42.07	2.31	0.19	2.33	0.3	5.24	63.71	8.31
4990	N	222.91	185.83	36.95	38.52	66.64	16.74	611.8	1179.39	1453.3
	B_w	470.13	585.6	9.33	1.92	8.0	3.39	43.76	1122.13	37.51
	B_c	17.5	55.78	1.44	0.29	1.6	0.51	7.3	84.42	5.63
4991	N	546.94	282.56	167.59	117.24	442.61	4.4	583.95	2145.29	4581.2
	B_w	191.31	1174.9	42.03	6.05	75.25	6.11	82.02	1577.67	169.9
	B_c	19.2	105.71	6.3	0.91	15.05	0.81	11.89	159.87	33.24
5004	N	767.01	268.05	181.0	62.97	452.3	18.44	274.4	1571.87	832.45
	B_w	401.43	1459.28	37.07	3.2	64.32	18.27	56.89	1976.14	27.38
	B_c	28.0	119.56	7.06	0.48	12.86	2.42	8.58	178.96	4.11

* This size group was not enumerated completely.

and 5048. In both cases *Chaetoceros compressus* formed ~75% of microphytoplankton. The maximum abundance of heterotrophic microphytoplankton was 0.23×10^9 cells/m^2 (9.4×10^3 cells/L) and was observed at station 5044 (Table 2).

Biomass of phytoplankton, 2011. The biomass of phytoplankton was low at practically all stations, which indicated the end of the vegetation season. The maximum values of the total wet biomass and carbon biomass of autotrophic phytoplankton (including picoplankton) constituted 3223 mg/m^2 and 356.8 mg C/m^2, respectively (128.9 mg/m^3 and 14.3 mg C/m^3) (station 5044, Table 2). The minimal values of the carbon biomass of phytoplankton were 7.6 mg C/m^3 and 7.3 mg C/m^3 and were recorded at stations 5043 and 5045, respectively. Microphytoplankton, which was represented by Bacillariophyceae and Dinophyceae, made the main contribution to the total biomass (Table 1). In the areas with the highest value of biomass (stations 5044 and 5048) *Chaetoceros compressus* was the main component of phytoplankton and formed 35–40% of the wet biomass and carbon biomass. The population of *C. compressus* was at the final stage of bloom and more than 50% of cells were found as spores. At these stations dinoflagellates formed ~40% of the wet biomass and carbon biomass. In the northern part of the transect (stations 5045 and 5046), nanophytoplankton formed a considerable part of the biomass along with microplankton due to the mass development of *Imantonia rotunda* and *Dicrateria* sp. 1.

The total wet biomass of all size groups of heterotrophic phytoplankton varied from 455 mg/m^2 (station 5047) to 1277 mg/m^2 (station 5048) (22.2 and 51.1 mg/m^3, respectively). The values of carbon biomass ranged within 81.8 mg C/m^2 (station 5044)

to 198.5 mg C/m^2 (station 5048) (3.2–7.9 mg C/m^3, respectively).

Quantitative characteristics of phytoplankton in 2007 (Table 3) were obtained without regard to picophytoplankton. Small cells of nanophytoplankton with a diameter from 3 to 5–6 μm were not completely enumerated in samples due to methodological reasons. The total abundance of phytoplankton in the upper 25-m layer varied in the surveyed area from 987×10^6 cells/m^2 (39.5×10^3 cells/L) (station 4989) to 2593×10^6 cells/m^2 (103.7×10^3 cells/L) (station 4987). The total wet biomass ranged from 612 mg/m^2 (24.5 mg/m^3) (station 4989) to 1976 mg/m^2 (79.0 mg/m^3) (station 5004); carbon biomass varied from 63.7 mg C/m^2 (2.5 mg C/m^3) at station 4989 to 179 mg C/m^2 (7.2 mg C/m^3) at station 5004. Heterotrophic species formed not more than 2% of the total abundance and 7–8% of the total wet biomass of phytoplankton. Heterotrophic species were not taken into account when calculating the total carbon biomass of phytoplankton.

The comparison of the quantitative characteristic of phytoplankton for 2 years was difficult because of the difference in enumeration of pico- and nano-size groups. In 2007, nanophytoplankton with a cell diameter of <5–6 μm were not completely taken into account, and the analysis of the materials of 2011 demonstrated that the cells of this diameter were numerous. This size group included most of Prymnesiophyceae, Cryptophyceae, and Prasinophyceae, as well as a group of unidentified cells. For example, during both years *Phaeocystis pouchetii* (Prymnesiophyceae) was detected in the form of mobile flagellate cells with a diameter from 2 to 6 μm. Thus, in samples collected in 2007, a considerable portion of the cells of the species was underestimated. The size group with the cell diameter of 2–5 μm included *Hemiselmis anomala* and most of the population of *Pyramimonas grossi*, which were also underestimated in materials of 2007. Underestimations of a considerable part of nanophytoplankton are evident when comparing values of the phytoplankton abundance obtained in the surveyed area during the both years. On average, the total number of cell of autotrophic phytoplankton (without picoplankton) was 3 times higher in 2011 than in 2007 and constituted 405.0×10^3 and 130.5×10^3 cells/L, respectively. The differences between the total wet biomass and the carbon biomass during these years were insignificant, 1.3 and 1.6 times, respectively, because the greatest contribution to the biomass was made by microplankton.

DISCUSSION

Our data make it possible to describe for the first time the structural features of phytoplankton in one of the key regions of the Kara Sea, namely in the area of the outer shelf, continental slope and the deepwater area adjacent to the St. Anna Trough. The processes occurring in the region have an impact on the interaction between ecosystems of the Arctic shelf and deepwater regions of the Arctic, and the formation of the biotopical boundaries. In addition, for the first time, the values of the ratio of abundance and biomass of different size groups of algae were obtained and the contribution of heterotrophic phytoplankton to the total abundance and the total biomass of the community at the end of the vegetation period were estimated for the Kara Sea basin.

The data of 2011 on all size groups of algae demonstrated the absolute dominance of the smallest fraction, picoplankton, in the total abundance of autotrophic phytoplankton and the prevalence of microphytoplankton in the formation of the total biomass (Tables 1, 2). The comparison of the abundance of autotrophic micro-, nano- and picoplankton demonstrated that the number of cells in each following group of algae of a smaller size increased by more than an order of magnitude.

Less distinct differences were found between the biomasses of three size groups of autotrophic phytoplankton. On average for the transect, the contribution of microphytoplankton to the total wet biomass of algae was 2.5 times greater than of nanophytoplankton and was 5 times greater than that of picoplankton. The carbon biomass of microphytoplankton was 1.4 times higher than biomass of algae of the nano-size group and 2.4 times higher than the biomass of picophytoplankton. The exceptions are of special interest. Thus, in the outer shelf at station 5043, the contribution of all three size groups of algae to the total wet biomass of the phytocene was similar and picoplankton dominated by the carbon biomass and constituted 43.8% (Table 2). Nanophytoplankton dominated in the carbon biomass (stations 5045 and 5046), and in the total wet biomass (station 5046) in the north in the deepwater part of the transect where the mass development of *Imantonia rotunda* and *Dicrateria* sp. 1 was observed (Table 2).

The abundance and biomass of heterotrophic phytoplankton was formed by nanophytoplankton at all stations. On average for the transect, the wet biomass of this size group of algae was 20 times higher than of picoplankton and 3.5 times higher than that of microphytoplankton. According to the bulk of data of 2011, the ratio of the total abundance of auto- and heterotrophic phytoplankton was 7 : 1, wet biomass was 2.5 : 1, and carbon biomass was 2.0 : 1.0 (Fig. 3).

The obtained materials make it possible to compare quantitative characteristics of phytoplankton in 2007 and 2011 and to consider the group of algae, such as diatoms, dinoflagellates, and coccolithophorids, which were reliably registered during the both studied years (Fig. 5, Table 4). The average abundance of diatom algae at all stations was 10.2×10^3 cells/L in 2007 and 15.5×10^3 cells/L in 2011. The wet biomass of diatoms was twice higher and the carbon biomass was 2.5 times higher in 2011 compared to 2007. The differ-

ences in the ratio of average values of abundance and biomass of diatoms can be explained by the fact that in 2007 the small-sized solitary *Chaetoceros gracilis* with a cell volume of not more than 150 μm^3 was the dominant species (>65% of the diatom cells) at half of the stations. In 2011, vegetative cells and spores of *Chaetoceros compressus* dominated among diatoms at all stations except the southernmost station on the transect. The species constituted >85% of the total abundance of diatoms at 4 stations. The average volume of vegetative cells of *C. compressus* varied from 1400 to 2400 μm^3, and the volume of spores ranged within 200–600 μm^3. The abundance and biomass of dinoflagellates were practically similar during the both years (Table 4) and juvenile forms and spores of dinoflagellates were dominant. *Heterocapsa triquetra*, *Scrippsiella trochoidea*, and several species of Gymnodinium were numerous at some stations during the both years. The low abundance and biomass of coccolithophorids were recorded in 2007 and 2011. The maximal abundance and biomass of this group were recorded in 2007 and constituted only ~9000 cells/L and 0.36 mg C/m^3, respectively.

In 2007, three regions with high quantitative characteristics of were defined along the transect. They are the southern shelf part of the transect, its northern deepwater part, and station 4987 above the continental slope (Figs. 6a, 6b). The distribution of the total abundance and the total biomass of cells were well distinguished in these regions. In 2011, two peaks of algae abundance were recorded at the southernmost station above the outer shelf (station 5043) and in the deepwater northern part of the transect (station 5046) (Figs. 6c, 6d). Relatively high biomasses of phytoplankton were recorded in the area of increasing depths and above the continental slope (stations 5044, 5046, and 5048).

The analysis of hydrophysical and hydrochemical data which were obtained simultaneously with phytoplankton samples demonstrated that in 2011 the boundary of surface waters which were strongly desalinated (to 18–19 psu) by the runoff of surface waters of the Ob and Yenisei rivers and the northern periphery of the surface desalinated lens with a salinity of 26 PSU shifted 70 km northwards. In 2011, the water temperature along the transect was 1.0–3.5°C higher than in 2007. Based on hydrophysical and hydrochemical data [1, 3, 5, 6] three pelagic biotopes were distinguished in the surveyed area, which differed in temperature, salinity, density, concentrations of nutrients, and vertical distribution of these parameters.

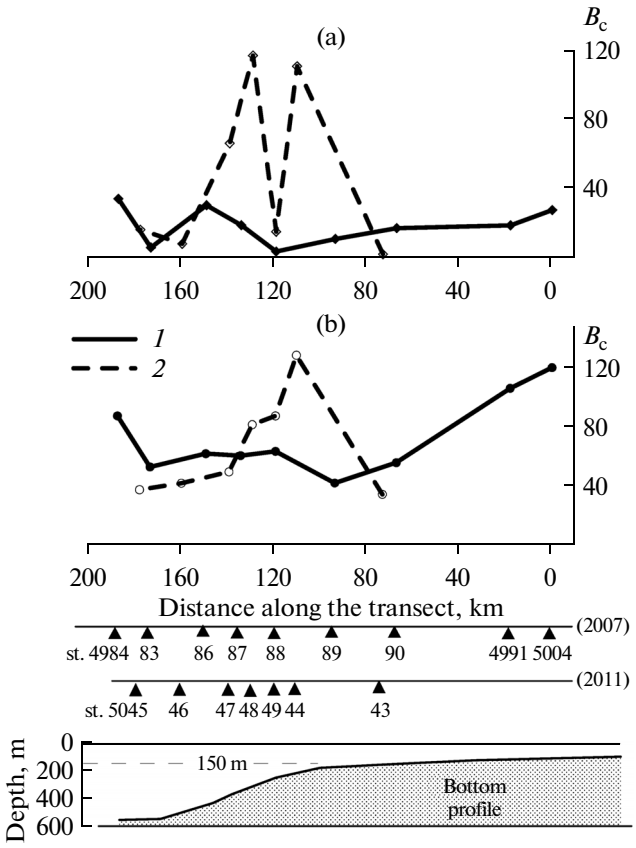

Fig. 5. Biomass (B_c, mg C/m^2) of diatom algae (a) and dinoflagellates (b) in the 0–25 m layer in 2007 (*1*) and 2011 (*2*); bottom profile (c).

Biotope 1 is the northern deepwater part of the surveyed region. In the biotope were stations 4983, 4984, 4986–4988 in 2007, and stations 5045–5047 in 2011, which were characterized by the uniform vertical dis-

Table 4. Average abundance (N, cells/L) and biomass (wet, B_w, mg/m^3; carbon biomass, B_c, mg/m^3) of diatoms and dinoflagellates and their minimal and maximal values in 2007–2011

Year	Bacillariophyceae			Dinophyceae		
	N min–max	B_w min–max	B_c min–max	N min–max	B_w min–max	B_c min–max
2007	10160 1450–30680	9.7 1.9–30.2	0.76 0.16–1.38	8790 5560–11550	32.1 17.7–47.0	2.88 1.68–4.78
2011	15535 790–40270	18.0 0.9–46.3	1.93 0.1–4.69	7470 3365–13480	28.7 13.7–55.2	2.62 1.38–5.11

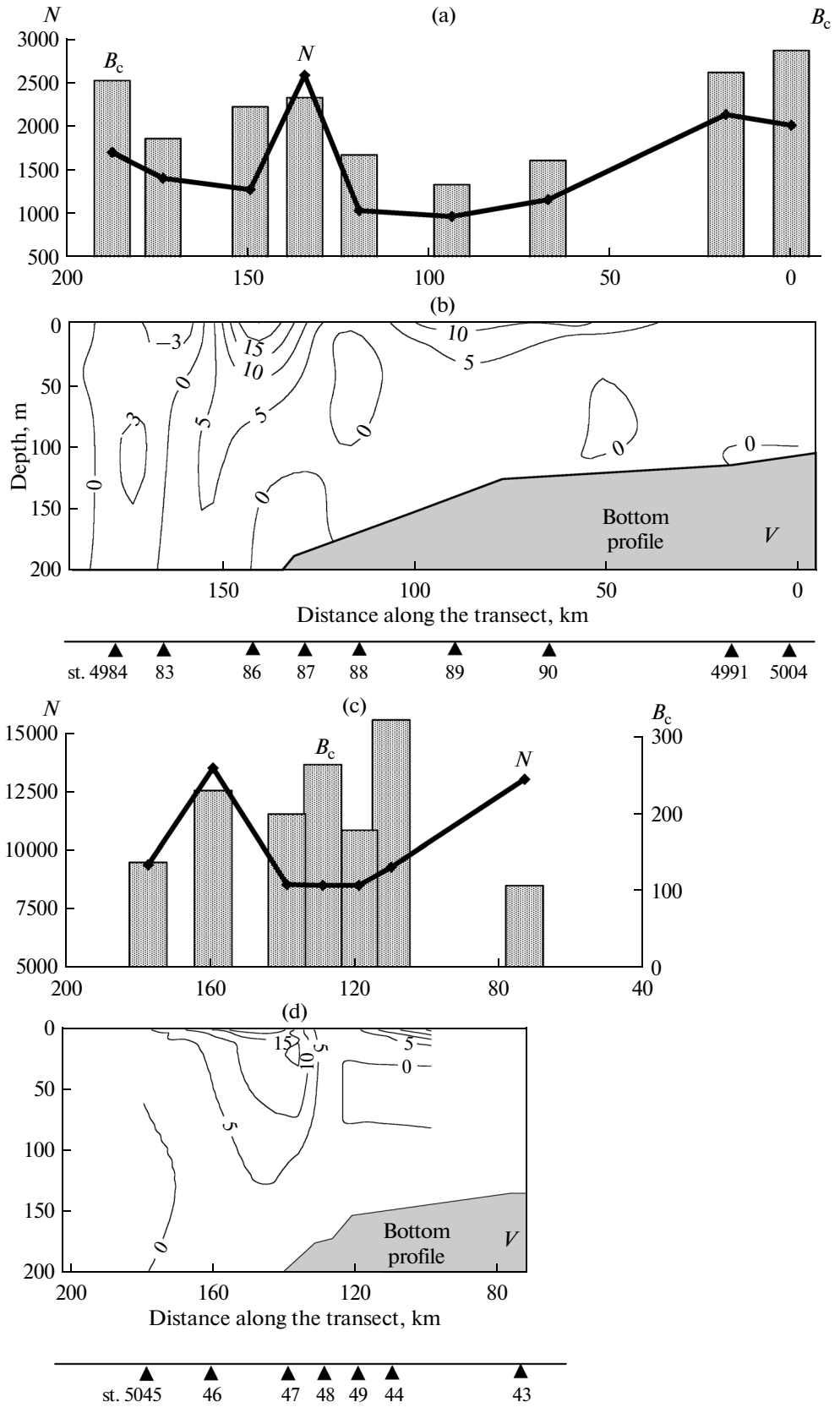

Fig. 6. Abundance ($N \times 10^6$, cells/L), carbon biomass (B_c, mg C/m^2) of phytoplankton in the 0–25 m layer and the structure of current fields (V, cm/s) along the transect of the outer Kara shelf, the continental slope, and a deepwater area in the western part of the St. Anna Trough in 2007 (a, b) and 2011 (c, d).

Table 5. Abundance ($N \times 10^3$ cells/L) and wet biomass (B_w, mg/m^3) of diatoms (D) and dinoflagellates (DF) and of the total phytoplankton (ΣPh) in three biotopes and the frontal zone (FZ) in 2007

Characteristics	Biotope 1			FZ			Biotope 2			Biotope 3		
	D	DF	SPh	D	DF	SPh	D	DF	SPh	D	DF	SPh
N	4.6	8.4	65.0	8.4	9.0	107.7	8.0	7.6	43.3	26.3	11.0	83.4
B_w	11.8	28.6	49.8	13.8	26.3	54.7	11.5	20.6	34.6	11.9	42.7	58.5

tribution of hydrophysical and hydrochemical parameters in the upper 40–50 m (Fig. 7, Table 5). Interannual differences in the environmental characteristics in the biotope were insignificant and concerned, mainly, the water temperature and salinity. In 2011, salinity was 0.5 psu lower and the temperature was 1.0–1.5°C higher than in 2007. According to the data of 2011, the species of the genus Prymnesiophyceae (with the dominance of *Imantonia rotunda, Dicrateria* sp.) constituted 51% of the total abundance and 31% of the total wet biomass of autotrophic phytoplankton in the northern biotope. *Prasinophyceae*, in particular *Pyramimonas grossii* and unidentified cells with a diameter of 3–5 μm, had a high abundance. *Resultor micron* (Pedinophyceae) was detected only in the northern biotope (Fig. 7). In 2007, unidentified cells and flagellates constituted ~70% of the total abundance; the biomass was, mainly, formed by dinoflagellates and diatoms (Table 5), which had higher species diversity compared to 2011.

The shelf edge and the upper part of the continental slope were defined as biotope 2. Within the limits of the biotope, stations 4989–4990 were studied in 2007 and stations 5048–5050 were studied in 2011. Biotope 2 is characterized by a shallow 4–6 m upper mixed layer, which was desalinated to 26–30 psu and an underlying layer of 5–6 m of sharply increased salinity, where S increased by 3–8 psu and δ_t increased by 2–6 conventional units (Fig. 7). In 2007 and 2011, relatively high concentrations of silica from 8 to 17 μg-atom/L were recorded in the upper mixed layer. The temperature of the upper layer of the sea was 3.0–3.5°C higher in 2011 than in 2007. The vertical distribution of temperature in the both years was distinguished by the presence of a cold intermediate subsurface layer (CSL). In 2007, at station 4989 the temperature at the depth of 4–5 m dropped below 0°C and reached its minimum, –1.6°C, between 12 and 15 m and increased to 0°C at a depth of 25 m. In 2011, the formation of CSL was observed only in the northern part of biotope 2. The temperature in the layer from 6 to 14 m decreased by 3.3°C, i.e. from 4.6 to 1.3, but at the depth of 16–20 m it increased to 3.5–4.0°C. In 2011, unidentified algae and Flagellate (34% of the total abundance of phytoplankton), Prymnesiophyceae (21%), and Cryptophyceae (21%) determined the qualitative and quantitative characteristics of the phytocene in biotope 2. *Phaeocystis pouchetii* with a motile stage constituted 75% of Prymnesiophyceae. *Hemiselmis anomala* and *Plagioselmis prolonga* constituted 95% of Cryptoceae. Dinoflagellates formed about 65% of the wet biomass and 36% of the carbon biomass of autotrophic algae (Fig. 7). In 2007, the biotope in the upper part of the continental slope was characterized by the lowest total abundance and biomass of phytoplankton (Table 5). The taxonomic structure of the phytocene was similar to that in the northern biotope 1, but the number of small diatoms increased compared to the northern biotope. When small cells dominated, the twofold increase in the diatom abundance did not result in a corresponding increase in the wet biomass of the group (Table 5).

The outer shelf in the southern part of the surveyed area was defined as biotope 3. The studies were conducted at stations 4991 and 5004 in 2007 and at station 5943 in 2011. The biotope was characterized by a strongly desalinated (to ~18 PSU) upper 10–12 m mixed layer, a relatively high temperature of the sea surface, 3–3.5°C in 2007 and 5°C in 2011, and a high concentration of silica 30–33 μg-atom/L due to the effect of the river runoff (Fig. 7). The vertical hydrophysical structure of the biotope in the upper 25 m differed between the years. In 2007, the layer with the conventional density 14–15, salinity of 18 psu, and temperature ~3°C occupied the upper 10 meters. Between 10 and 15 meters the density increased to 26–27 conventional units, and the temperature dropped to –1.5°C. In 2011, the density increased gradually from 14 in the surface layer to 26.5 conventional units at the depth of 25 m, salinity increased from 18 to 33 psu, the temperature increased from 5°C in the surface layer to 7°C at a depth of 15 m and then gradually decreased to 2°C at a depth of 25 m. The qualitative structure of phytoplankton over the outer shelf differed significantly between 2007 and 2011. This affected the quantitative parameters of diatoms and dinoflagellates (Fig. 7, Table 5). In 2007, diatoms and unidentified cells (including Flagellatae > 5 μm) constituted 32% and 42%, respectively, of the total abundance of algae. Dinoflagellates formed 73% of the total wet biomass and 67% of the carbon biomass of autotrophic phytoplankton. The high abundance and low biomass of diatoms were the result of the dominance (~90% of the abundance of the group) of the small-sized species

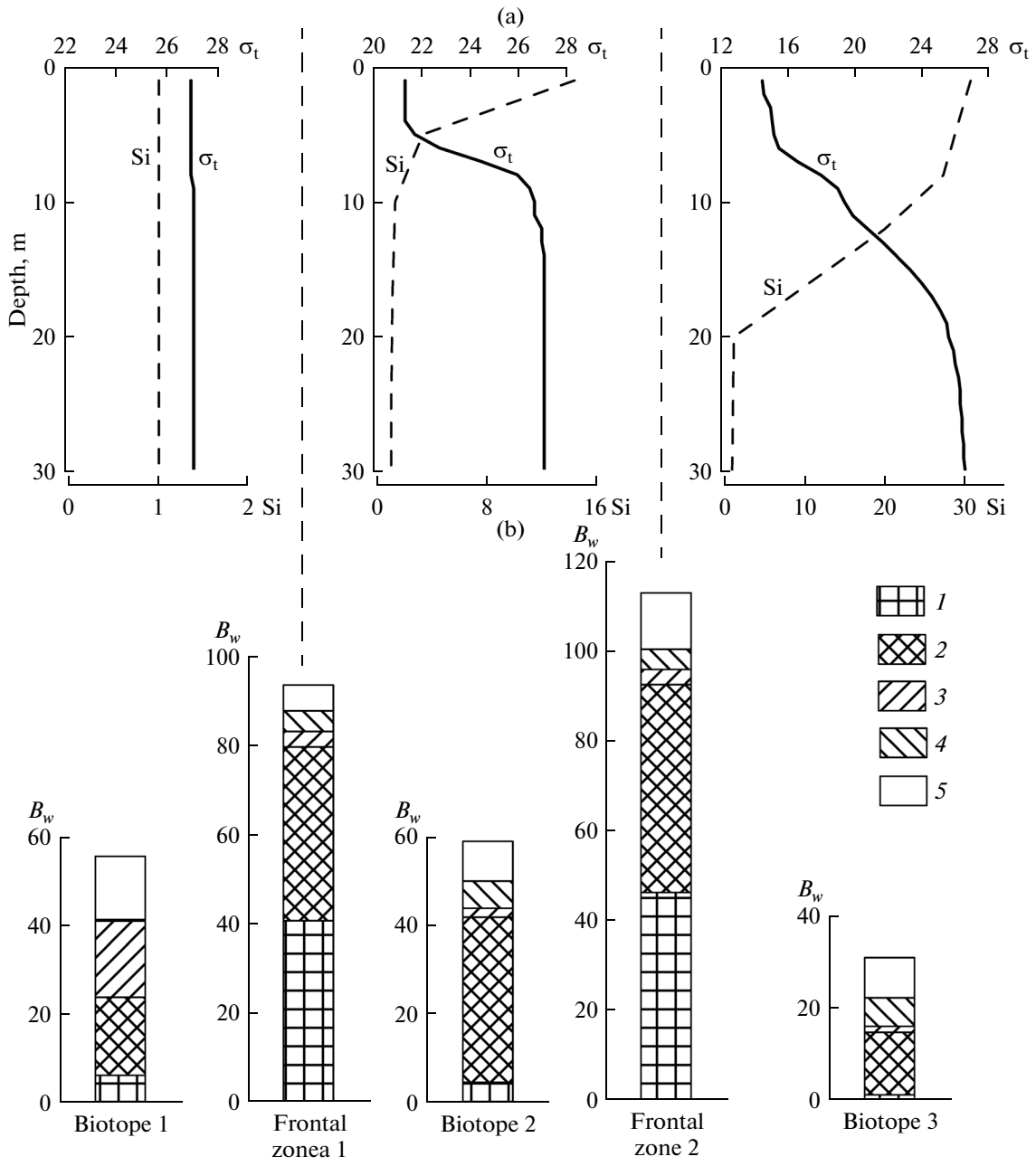

Fig. 7. Vertical distribution of density (δ_t) and silica (μmg-atom/L), (a), the wet biomass of phytoplankton (B_w, mg/m^3) and the contribution of the dominant taxonomic groups of algae in the upper 25 m in different pelagic biotopes and frontal zones dividing them into biotopes in the northwestern Kara Sea, (b). *1*, Bacillariophyceae; *2*, Dinophyceae; *3*, Prymnesiophyceae; *4*, Cryptophyceae *5*, the rest.

Chaetocerus gracilis. In 2011 two species of Cryptophyceae, *Hemiselmis anomala* and *Plagioselmis prolonga*, formed 42% of the total abundance of cells. The contribution of diatoms did not exceed 1%. The main contribution to the biomass of the phytocene was made by Cryptophyceae and unidentified cells which together formed 55% of the total wet biomass of autotrophic algae (Fig. 7). In addition, the highest for the surveyed area abundance of autotrophic picophytoplankton 218 × 10^9 cells/m^2 (8.7 × 10^6 cells/L) was recorded in the biotope of the outer shelf in 2011. This group contributed 35.3% to the total wet biomass of autotrophic phytoplankton.

In our opinion, special attention should be paid to the analysis of the effect of boundary frontal zones dividing the biotopes on the phytoplankton community. Sharp changes in the characteristics of the environment in frontal zones was the result of dynamic

processes. Changes in the structural parameters of phytocenoses in frontal zones were more distinctly expressed in 2011 (Fig. 7). Frontal zone 1, which divides the northern deepwater biotope 1 and biotope 2 in the area of the continental slope, was associated with the southern boundary of the flow of Atlantic waters, which is clearly seen in the structure of current fields (Figs. 6b, 6d) [4]. Station 5048 in frontal zone 1 was characterized by a high total wet biomass of phytoplankton and a high contribution (43.5%) of diatoms to the biomass of the community (Fig. 7). This frontal zone was associated with the northern periphery of the surface water lens strongly desalinated by the river runoff, where the depth of the upper mixed layer decreased to 1–2 m [1, 3]. The differences in phytocenoses inhabiting different biotopes were less distinct in 2007. Unidentified cells prevailed, according to the number of cells in all biotopes. The biomass was formed by dinoflagellates and diatoms in all biotopes. As is seen from Table 5, the ratio of abundance and biomass demonstrates the changes in the size structure of diatoms as we moved southwards, which was determined by changes in the taxonomic structure of the diatom community. The maximal abundance of phytoplankton due to mass growth of unidentified forms of planktonic algae was recorded at station 4987 located in the frontal zone that divided the deepwater biotope and the biotope of the continental slope and was associated with the periphery of the slope current (Figs. 6a, 6b).

CONCLUSIONS

For the first time, the phenomenon of the existence of several biotopes with specific abiotic conditions and inhabited by phytoplankton communities differing in species composition, dominating groups of algae and quantitative characteristics has been revealed in the open part of the Kara Sea. It is important that such biotopical diversity exists within the areas of the basin that extend only 100–200 km latitudinally. This is evidence for the necessity to take into account the mesoscale (from 10 km) features of the pelagic environment, when studies are conducted in regions of complex hydrophysical structure and water dynamics to obtain adequate estimates of the composition and quantitative characteristics of regional phytocenoses.

The materials which were obtained in the course of our studies made it possible to detect the effect of frontal zones in the open part of the Kara Sea basin on the structural parameters of phytoplankton. The relatively high total biomass of phytoplankton, the high abundance of diatom algae and the prevalence of one species in the frontal zones makes it possible to suggest the presence in the regions of the mechanisms that ensure the local availability of "new" nutrients and intensive growth of algae during most of the vegetation season. This is confirmed by the maximal values of the primary production in the autumn period [4]. The periodical input of nutrients to the upper layer of the sea in frontal zone 2 at the outer boundary of the surface lens of desalinated waters can be caused by the wind action and erosion of the shallow pycno-halocline underlying the surface. At the end of September we observed the late stage of a *Chaetoceros diadema* "bloom" at the edge of the surface desalinated lens in the southwestern Kara Sea under similar conditions [8]. The mechanism of the impact of winds on the vertical structure of the pelagic biotope and the nutrient regime of the euphotic layer at the periphery of the desalinated lens in the Kara Sea may be similar to the mechanism we described for coastal structural fronts [10, 11].

Interannual differences in the structure of phytoplankton communities in the surveyed areas of the Kara Sea, which were determined while comparing the phytocene components reliably estimated during both years, can be the result of various factors. Such differences can be caused by differences in the course of seasonal processes demonstrated by differences in temperature and salinity of the euphotic layer in the regions under study. One reason may be changes in abiotic conditions caused by a 70-km shift to the north of the outer boundary of a surface water lens strongly desalinated by the river runoff in 2011. All these factors determine the possibility of the predominant development and, in some cases, the "bloom" of different species of algae, which constitute part of a particular seasonal complex in different years.

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