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EXPERIMENTAL ARTICLES

Picophytoplankton Abundance in the Velikaya Salma Strait, White Sea

T. A. Belevich[1] and L. V. Ilyash

Moscow State University

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Abstract—In July–August 2009, the abundance of picophytoplankton (Pico) in the Velikaya Salma strait varied from 3.4×10^6 to 19.4×10^6 cells/L, while its biomass (B) was 0.8–3.3 mg C/m^3. In August 2010, Pico abundance was significantly higher (up to 216×10^6 cells/L and 36.8 mg C/m^3). Pico consisted mainly of cyanobacteria. It constituted 13 (2009) to 28% (2010) of the total phytoplankton biomass. In April 2010, Pico numbers varied from 0.1×10^6 to 0.22×10^6 cells/L and its biomass was 0.05–0.28 mg C/m^3. Picoeukaryotes were predominant. Pico constituted not more than 2.7% of the phytoplankton biomass. In the ice column, the integrated Pico abundance was 430×10^6 cells/m^2 and the integrated biomass was 365 μg C/m^2.

Keywords: picophytoplankton, picocyanobacteria, picoeukaryotes, White Sea.

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Picophytoplankton (Pico) comprises cyanobacteria and eukaryotic algae with cell size below 2 μm [1] or below 3 μm, according to more recent publications [2, 3]. These minute photoautotrophs may contribute a major part of the total biomass and production of phytoplankton, especially in oligotrophic environments or in mesotrophic waters during the periods of low abundance of microphytoplankton. The calculated contribution of Pico in the total phytoplankton biomass and primary production in the World Ocean is 8 and 39%, respectively [4]. Abundance of Pico in the White Sea has been assayed only in the Chupa inlet of the Kandalaksha Bay in June–early July [5] and in April [6]. No information on Pico abundance is available for other parts of the sea and other periods of the vegetation season.

The present work provides the data on abundance and biomass of picophytoplankton, as well as on the species composition, abundance, and biomass of nano- and microphytoplankton in the Velikaya Salma strait of the Kandalaksha Bay in April and in July–August.

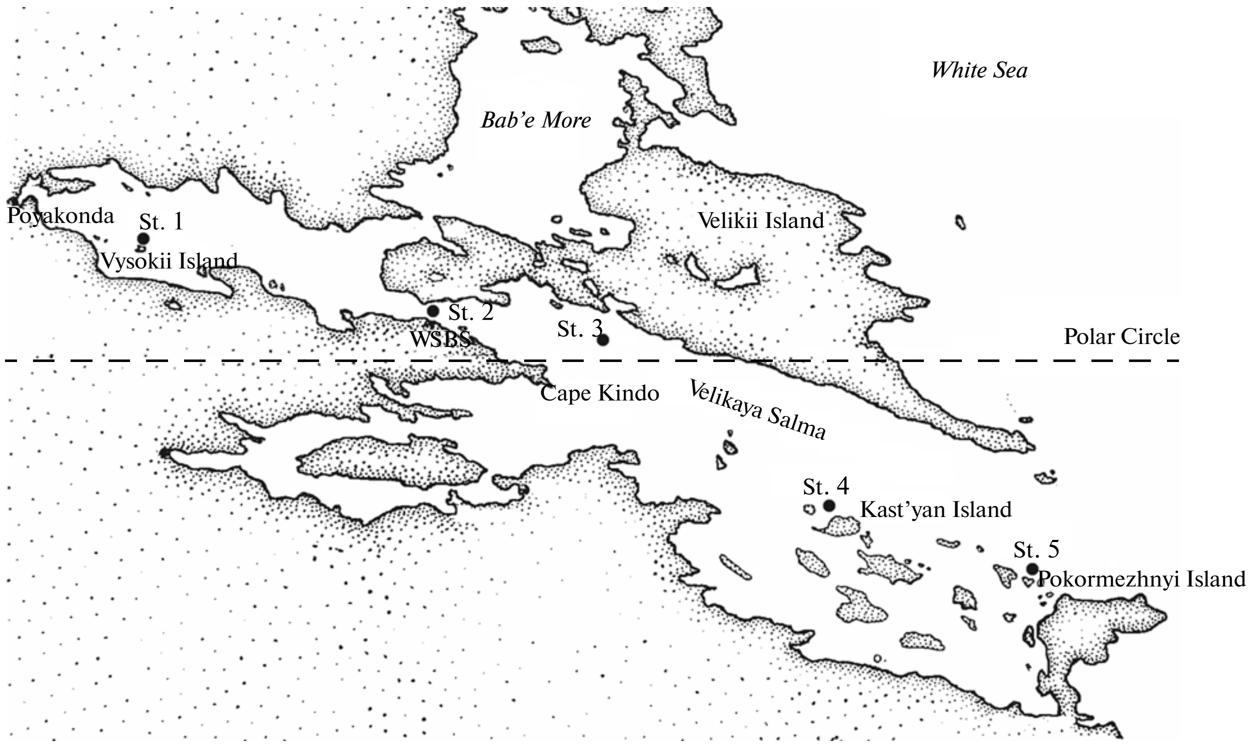
MATERIALS AND METHODS

The investigation was carried out in 2009–2010 in the Velikaya Salma strait of the Kandalaksha Bay, White Sea, using the White Sea Biological Station, Moscow State University, as a base (66°43′ N, 33°08′ E). For assessment of the temporal dynamics of the phytoplankton, water samples were collected from July 26 to August 16, 2009 with a 5-L bathometer from the depth of 2.5 m at station 2, located in the middle of the strait opposite of the biological station (figure). For assessment of the spatial variability of the phytoplankton, samples from 2.5-m depth were collected at four stations during the same period (figure). For assessment of the vertical distribution of the phytoplankton, samples from the depths of 0, 2.5, 5, 10, 15, 25, and 50 m were collected at station 3 on August 8, 2009 and August 19, 2009.

For assessment of the composition and abundance of the early spring phytoplankton, samples from the surface layer and 1 m depth were collected from April 14 to April 20, 2010 from the pier of the biological station. The Velikaya Salma strait was free of ice, with only an edge of fast shore ice not exceeding 5 m. The ice cover was disrupted by a deep storm two weeks before the sampling period, and the ice was removed from the strait by tidal currents. Only one core of fast ice was therefore collected at the point 500 m to the west from the pier of the biological station with 0.5-m depth. The core was collected using a titanium 15-cm corer. It was divided into three parts: the upper (0–26 cm), consisting of turbid, matt ice of snow origin; the medium (26–34 cm), consisting of gray semitransparent ice with embedded particles of bottom sediments, *Fucus*, and filamentous algae; and the lower one (34–52 cm), formed by crystalline ice of water origin with embedded particles of bottom sediments and plant debris. The core fragments were melted in the laboratory for 12 h at room temperature.

For quantitative interpretation of the samples, the linear sizes of the algae belonging to picophytoplankton, nanophytoplankton, and microphytoplankton

[1] Corresponding author; e-mail: 3438083@list.ru



Location of the sampling stations in the Velikaya Salma strait.

were accepted as 0.2–3, 3–20, and 20–200 μm, respectively, according to [1–3].

The numbers of picophytoplankton were assessed using the previously described method [5]. The water sample (10 mL) was placed into a filtration funnel, supplemented with the saturated solution of primulin, incubated for 5–7 min, and fixed with 2% glutaraldehyde. Nuclear filters (0.12 μm pore diameter) prestained with Sudan black were used for filtration. The cells were counted under a LeicaDM2500 epifluorescence microscope at ×100 × 10 × 1.3 magnification. Depending on the concentration of the cells, 30 to 50 microscope fields were examined. In the course of cell counts, the "type" of fluorescence (orange for cyanobacteria and red for eukaryotic algae) and the cell size were determined. Cell volumes were calculated as volumes of the relevant geometrical bodies [7]. Carbon content of the cells was determined from cell volumes using the relevant allometric relations [8]. Apart from picoplankton, the cells 3–8μm in size, i.e., belonging to nanophytoplankton, were enumerated.

For assessment of abundance of microphytoplankton and nanophytoplankton with the cells over 8 μm, water samples (0.7–3.2 L) were concentrated by reverse filtration (2 μm pore diameter) and fixed with Lugol's solution. The concentrated samples were examined in a 0.05 mL chamber under a Mikromed 3 microscope with × 40 ×10 × 0.65 magnification. The linear size of the cells was determined with an ocular micrometer. Cell volumes were calculated as volumes of the relevant geometrical bodies [7]. Carbon content of the cells was determined from cell volumes using the relevant allometric relations and considering the taxonomic position of the algae [9]. The higher taxonomic ranks of eukaryotes are presented in accordance with the taxonomic system given in [10].

RESULTS

Temporal dynamics of the phytoplankton. Picophytoplankton abundance at station 2 in July–August 2009 varied from 4.8×10^6–13.3×10^6cells/L, with the average value of $9.1 \pm 3.1 \times 10^6$ cells/L. Picophytoplankton contained mostly cyanobacteria. The number of eukaryotic algae was, on average, one order of magnitude lower than the number of prokaryotes. The average Pico biomass was 1.6 ± 0.63 mg C/m^3. Pico contributed 2 to 13% to the overall biomass of phytoplankton (Table 1). The Pico contribution was highest in late June, at the lowest abundance of micro- and nanophytoplankton. During three weeks of observation, the Pico biomass varied within the same range (CV = 34%) as the biomass of micro- and nanophytoplankton (CV = 35%). Within the micro- and nanophytoplanktonic community, both the biomass and the structure of the phytoplankton varied, so that the dominant and abundant (contributing over 10% to the total biomass) algal species differed (Table 1). Since late July, the biomass of the diatom *Skeletonema costatum* increased, while the abundance of mixotrophic

Table 1. Biomass (mg C/m^3) of picophytoplankton (Pico) and micro- and nanophytoplankton (MNP), the total phytoplankton biomass (B_c), contribution of picophytoplankton to the total phytoplankton biomass (Pico, %), the dominant and abundant species of nano- and microphytoplankton, and their contribution (in parentheses) to the total phytoplankton biomass in 2009

Station no.	Date	Pico	MNP	B_c	Pico, %	Dominant and abundant species of nano- and microphytoplankton
2	26.07	1.8	16.2	18.0	10.1	su (40), *Heterocapsa rotundata* (21)
	29.07	1.8	11.7	13.5	13.1	su (31), *Heterocapsa rotundata* (15)
	01.08	1.9	26.4	28.4	6.8	su (31), *Skeletonema costatum* (17)
	04.08	2.1	28.8	30.9	6.9	*Skeletonema costatum* (15), *Chaetoceros* sp. 1 (13), *Heterocapsa rotundata* (13), su (10)
	07.08	2.4	40.2	42.6	5.7	su (24), *Skeletonema costatum* (10), *Melosira nummuloides* (10)
	10.08	1.5	26.2	27.6	5.3	su (15), *Skeletonema costatum* (11)
	13.08	0.9	26.6	27.4	3.1	*Ceratium fusus* (16)
	16.08	0.8	36.5	37.3	2.3	*Ceratium fusus* (11), *Scrippsiella trochoidea* (11)
3	02.08	1.2	26.0	27.2	4.4	*Heterocapsa rotundata* (19), *Skeletonema costatum* (12)
4	02.08	2.8	40.9	43.7	6.5	su (29), *Heterocapsa rotundata* (13)
5	08.08	1.9	32.9	34.8	5.4	su (32), *Heterocapsa rotundata* (14), *Ceratium fusus* (14)
1	15.08	2.0	48.0	50.0	4.1	su (19), *Alexandrium minutum* (11), *Ceratoneis closterium* (10)

Note: "su" stands for small unidentified flagellates and coccoid algae.

dinoflagellates *Ceratium fusus* and *Scrippsiella trochoidea* increased in the second decade of August. A total of 92 algal species was found among the micro- and nanophytoplankton. *Bacillariophyta* (64 species) and *Dinozoa* (22 species) were the most diverse taxa. Members of *Chrysophyceae*, *Dictyochophyceae*, and *Cyanobacteria*, were also found, as well as unidentified small flagellates and coccoid algae, cysts of dinoflagellates and *Chrysophyceae*, and diatom spores.

Spatial distribution of phytoplankton. Along the Velikaya Salma strait (stations 1 and 3–5), the number and biomass of Pico varied within the range observed at station 2 during three weeks of observation. At station 4, however, Pico abundance was higher (17×10^6 cells/L and 2.8 mg C/m^3). Cyanobacteria predominated within the picophytoplankton. The numbers of eukaryotic Pico were on average two orders of magnitude lower than prokaryotic abundance. Pico contributed to not more than 7% of the total phytoplankton biomass. The biomass and the dominant species of micro- and nanophytoplankton at stations 3–5 were similar to those observed at station 2 at the relevant time. The dominant micro- and nanophytoplankton species at station 1 differed from those at station 2, and their biomass was higher. In general, the spatio-temporal variability (for all stations throughout the observation period) for the Pico (CV = 33%) and micro- and nanophytoplankton biomass (CV = 35%) correlated with the temporal variability at station 2.

Vertical distribution of phytoplankton. In 2009, the water temperature decreased from 20.6°C in the surface layer to 18.1°C at 15 m and then remained constant to 50-m depth. The Pico abundance varied from 3.4×10^6 cells/L (5 m) to 19.4×10^6 cells/L (50 m). The highest Pico biomass was observed at the depths of 2.5 and 50 m, while the lowest one occurred at 5 m (Table 2). The biomass of micro- and nanophytoplankton was almost uniformly distributed within the upper 5-m layer and was somewhat lower within the 10–15-m layer. Its variation with depth was less pronounced (CV = 28%) than that of picophytoplankton (CV = 49%). Unidentified small flagellates and coccoid algae contributed most significantly to the total biomass of phytoplankton throughout the water column.

In 2010, the water temperature almost did not change with depth (12.6°C in the surface layer and 12.3°C at the depth of 50 m). While the temperature was lower than in 2009 and no stratification was observed, the Pico numbers were higher by an order of magnitude: from 94 × 10^6 cells/L (5 m) to 216 × 10^6 cells/L (0 m). Similar to 2009, cyanobacteria predominated among the Pico throughout the water column. Although the biomass of micro- and nanophytoplankton was higher than in 2009, the contribution of Pico was more significant. The highest contribution of Pico was observed in the surface layer, while the lowest was found at the 5-m depth, similar to 2009. This was the depth where the highest biomass of micro- and nanophytoplankton was observed. Among the micro- and nanophytoplankton, 80 algal species were identified. Diatoms (46 species) and dinoflagellates (24 species) were the major groups, while members of *Chrysophyceae, Dictyochophyceae, Cyanobacteria*, and *Euglenozoa* were also found, as well as small unidentified flagellates and coccoid algae, *Chrysophyceae* cysts, and diatom spores. The biomass of micro- and nanophytoplankton varied with depth to a lesser degree (CV = 17%) than the Pico biomass (CV = 29%) and peaked at 25 m. At all depths, the diatoms *Ditylum brightwellii* and *Chaetoceros affinis* were the major components of the total biomass.

Early spring phytoplankton. Abundance of Pico varied from 0.1 × 10^6 to 0.22 × 10^6 cells/L. The numbers of picoeukaryotes, the predominant group, varied from 0.05 × 10^6 to 0.20 × 10^6 cells/L. The highest values of Pico numbers and biomass were found in the ice-free water area during the low tide (Table 3). The average biomass of Pico was 0.13 ± 0.10 mg C/m^3. The picoeukaryote biomass varied from 0.03 to o.28 mg C/m^3, i.e., it constituted 77–99% of the Pico biomass. Its contribution to the total biomass of phytoplankton did not exceed 2.7%. The micro- and nanophytoplankton were represented by 70 algal species. The diatoms (57 species) exhibited the highest diversity. Members of the *Dinozoa, Chlorophyta, Cyanobacteria*, and *Euglenozoa* were also present, as well as small unidentified flagellates and coccoid algae and dinoflagellate cysts. The highest abundance of micro- and nanophytoplankton was found in the thin layer of under-ice water. The algae with ice as the preferred habitat prevailed among the micro- and nanophytoplankton. Its biomass was more variable (CV = 128%) than the Pico biomass (CV = 82%).

The highest numbers and biomass of picophytoplankton were observed in the lower part of the ice core (Table 4). Eukaryotes predominated among Pico in both numbers and biomass. Their share in all the ice layers was almost constant, about 80% of the total Pico biomass.

DISCUSSION

Picophytoplankton of the Velikaya Salma strait consisted of cyanobacteria and eukaryotic algae. Since species identification of the picoplankton forms requires molecular genetic approaches, species diversity of the Pico in this environment will not be discussed in the present work. According to the literature data, picocyanobacteria of the polar waters belong almost exclusively to the genus *Synechococcus* [11]. The species diversity of picoeukaryotes is much higher and includes tens of species of various divisions of algae [3]. *Prasinophyta* of the genera *Micromonas, Bathycoccus*, and *Ostreococcus* are the most abundant ones in the polar and temperate waters [12, 13]. These algae are probably present among the eukaryotic picoplankton of the White Sea.

Among the picophytoplankton of the strait, cyanobacteria predominated in summer, while picoeukaryotes, in early spring. Ice also contained a higher relative abundance of picoeukaryotes. Water temperature is considered among the major factors responsible for the relative abundance of cyanobacteria and picoeukaryotes [13, 14]. Cyanobacteria were not retrieved from the water of the Arctic Ocean [12, 15], while picoeukaryotes were numerous in this region.

Abundance of the picophytoplankton in the Velikaya Salma strait in July–August 2009 varied within the same range as observed in various Arctic areas [2, 12, 13, 15–17], while the Pico number in August 2010 was significantly higher, corresponding to the values reported for subpolar sites [18]. The biomass of micro- and nanophytoplankton was also above the characteristic values for the Kandalaksha Bay in late summer [19]. According to the literature data, *Synechococcus* abundance depends on availability of inorganic nutrients and is higher in mesotrophic waters [20]. During the late summer stratification in the White Sea, the phytoplankton is limited by nitrogen deficiency and its biomass, developing mainly due to regenerated nitrogen, is not high [19]. Such local hydrophysical phenomena (in space and time) as strong, wind-induced mixing disrupting the thermocline or intense tidal mixing may, however, result in the penetration of inorganic nutrients into the upper water layers [21]. Unusually high abundance of pico-, micro-, and nanophytoplankton in August 2010 probably resulted from such local enrichment of the upper photic layer due to the storms of the second decade of August. The absence of stratification in the water column and lower water temperature in August 2010 support the suggestion that deep mixing enriched the upper layers with inorganic nutrients. Moreover, the possible effect of the weather anomalies of the summer 2010 on development of phytoplankton should not be ruled out [22]. In other subpolar regions, year-to-year variability in Pico abundance was also revealed [18].

The range of picophytoplankton abundance in the Velikaya Salma strait in April was two orders of magnitude lower than the value of the under-ice picophytoplankton measured in April in the Chupa inlet of the Kandalaksha Bay [6]. The total phytoplankton abundance in the Chupa inlet was also significantly higher (690 mg C/m^3). During our observations, both the Pico and micro- and nanophytoplankton had probably not reached the peak of spring bloom.

Table 2. Biomass (mg C/m^3) of picophytoplankton (Pico) and micro- and nanophytoplankton (MNP), the total phytoplankton biomass (B_c), contribution of picophytoplankton to the total phytoplankton biomass (Pico, %), the dominant and abundant species of nano- and microphytoplankton, and their contribution (in parentheses) to the total phytoplankton biomass at different depths at station 3 in 2009 and 2010

Depth, m	Pico	MNP	B_c	Pico, %	Dominant and abundant species of nano- and microphytoplankton
08.08.2009					
0	1.3	41.0	42.3	3.1	su (16), *Heterocapsa rotundata* (16), *Chaetoceros radicans* (13)
2.5	3.0	40.4	43.4	6.8	su (29), *Chaetoceros radicans* (13), *Heterocapsa rotundata* (11)
5	0.6	43.4	44.1	1.4	su (15), *Chaetoceros radicans* (12), *Heterocapsa rotundata* (10), *Chaetoceros* sp. (10)
10	1.5	24.6	26.1	5.7	su (16), *Heterocapsa rotundata* (14)
15	1.6	20.4	21.9	7.2	su (17), *Chaetoceros radicans* (12)
25	2.2	34.0	36.2	6.0	su (26), *Heterocapsa rotundata* (11), *Skeletonema costatum* (10)
50	3.3	47.7	51.0	6.4	su (32), *Heterocapsa rotundata* (11)
19.08.2010					
0	36.8	93.6	130.4	28.2	*Ditylum brightwellii* (30), *Chaetoceros affinis* (19)
2.5	29.6	100.4	130.0	22.7	*Ditylum brightwellii* (45), *Chaetoceros affinis* (19)
5	16.3	120.5	136.8	11.9	*Ditylum brightwellii* (47), *Chaetoceros affinis* (14), *Coscinodiscus concinnus* (10)
10	23.4	121.2	144.6	16.2	*Ditylum brightwellii* (46), *Chaetoceros affinis* (26)
15	20.6	134.8	155.5	13.3	*Ditylum brightwellii* (39), *Chaetoceros affinis* (20), *Coscinodiscus concinnus* (11)
25	19.9	136.4	156.3	12.7	*Ditylum brightwellii* (52), *Chaetoceros affinis* (18)
50	22.4	90.7	113.1	19.8	*Ditylum brightwellii* (46), *Chaetoceros affinis* (22)

Note: "su" stands for small unidentified flagellates and coccoid algae.

Pico contributed 1.4–28.2% and 0.1–2.7% to the phytoplankton biomass in summer and spring, respectively, which is within the range reported for other polar regions [2, 15]. In April, the average contribution of picophytoplankton to the total biomass of phytoplankton in the Velikaya Salma strait was 0.9 ± 1.2%, which is less than the Pico contribution in the Chupa inlet in a similar period (6%) [6].

During the three weeks of summer observations, the temporal variation in abundance of picophytoplankton was the same as that for micro- and nanophytoplankton. While cyanobacteria always predominated in the picophytoplankton, the succession of the dominant and abundant algal species occurred in the micro- and nanophytoplankton, which generally coincided with the phytoplankton dynamics of the Kandalaksha Bay [19].

In summer, the highest biomass of picophytoplankton was observed at the depths of 2.5 and 50 m in 2009 and in the surface layer in 2010. In 2010, the biomass of picophytoplankton varied with depth to a lesser degree than in 2009. The highest Pico abun-

Table 3. Biomass (mg C/m^3) of picophytoplankton (Pico) and micro-and nanophytoplankton (MNP), the total phytoplankton biomass (B_c), contribution of picophytoplankton to the total phytoplankton biomass (Pico, %), the dominant and abundant species of nano- and microphytoplankton, and their contribution (in parentheses) to the total phytoplankton biomass in April 2010

Date	Sampling site	Pico	MNP	B_c	Pico, %	Dominant and abundant species of nano- and microphytoplankton
14.04	Below fast ice, at the point of ice coring	0.09	115.6	115.7	0.1	*Nitzschia frigida* (40), *Ulothrix* sp. (10)
16.04	From the pier, depth 1 m	0.09	25.8	25.9	0.4	*Melosira arctica* (20), *Detonula confervacea* (17)
17.04	From the pier, depth 0 m low tide	0.28	9.8	10.1	2.7	*Navicula vanhoeffenii* (16), *Fragilariopsis oceanica* (11)
18.04	From the pier, depth 0 m, high tide	0.05	8.2	8.3	0.6	*Navicula vanhoeffenii* (18), *Fragilariopsis oceanica* (15)

dance in both the surface layers and the layers below the thermocline has been reported for other Arctic regions [15].

In the fast ice of the Velikaya Salma strait, the highest Pico abundance was found in the lower ice layers. Eukaryotes predominated among the picophytoplankton in both numbers and biomass. The highest abundance of eukaryotic picoalgae in the lower part of the ice was also observed at one of the coastal station of the Chupa inlet, while in other stations, the middle part of the ice core contained the most picoeukaryotes [23].

In conclusion, we want to stress the following. The relative contribution of picophytoplankton to the total phytoplankton biomass of the White Sea in spring and summer does not exceed 28.2%. However, according to some authors [24], the modern climatic trends in the Arctic with increasing water temperature result in increasing abundance of picophytoplankton and decreasing abundance of nanophytoplankton. If this tendency holds for the White Sea, the role of picophytoplankton in the White Sea ecosystem will increase, requiring further investigation of the smallest photoautotrophs.

Table 4. Biomass (B) and number (N) of picophytoplankton and its contribution to the integral number (N, %) and biomass (B, %) in different ice layers in April 2010

Ice layers, cm	N × 10^6, cells/m^2	B, μg C/m^2	N, %	B, %
0–26	59	44	14	12
26–34	76	66	18	18
34–52	295	255	69	70
Total below 1 m^2	430	365	100	100

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REFERENCES

1. Sieburth, J.M., Smetacek, V., and Lenz, J., Pelagic Ecosystem Structure: Heterotrophic Compartments of the Plankton and Their Relationships to Plankton Size Fractions, *Limnol. Oceanogr.*, 1978, vol. 23, pp. 1256–1263.
2. Moreira-Turcq, P.F., Cauwet, G., and Martin, J.M., Contribution of Flow Cytometry to Estimate Picoplankton Biomass in Estuarine Systems, *Hydrobiologia*, 2001, vol. 462, pp. 157–168.
3. Moon-van der Staay, S.Y., De Wachter, R., and Vaulot, D., Oceanic 18S rDNA Sequences from Picoplankton Reveal Unsuspected Eukaryotic Diversity, *Nature*, 2001, vol. 409, pp. 607–610.
4. Agawin, N.S.R., Duarte, C.M., and Agusti, S., Nutrient and Temperature Control of the Contribution of Picoplankton to Phytoplankton Biomass and Production, *Limnol. Oceanogr.*, 2000, vol. 45, p. 1891.
5. Il'yash, L.V., Picobacterioplankton of the Kandalaksha Bay, White Sea, *Vestnik Moskovsk. Univ.*, *Ser. 16. Biology,* 1998, no. 2, pp. 49–52.
6. Rat'kova, T.N., Sazhin, A.F., and Kosobokova, K.N., Unicellular Inhabitants of the White Sea Underice Pelagic Zone during the Early Spring Period, *Okeanology*, 2004, vol. 44, no. 2, pp. 240–246.
7. Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., and Zohary, T., Biovolume Calculation for Pelagic and Benthic Microalgae, *J. Phycol.*, 1999, vol. 35, pp. 403–424.
8. Verity, P.G., Robertson, C.Y., Tronzo, C.R., Andrews, M.G., Nelson, J.R., and Sieracki, M.E., Relationship between Cell Volume and the Carbon and Nitrogen Content of Marine Photosynthetic Nano-

plankton, *Limnol. Oceanogr.,* 1992, vol. 37, pp. 1434–1446.

9. Menden-Deuer, S. and Lessard, E.J., Carbon to Volume Relationships for Dinoflagellates, Diatoms, and Other Protist Plankton, *Limnol. Oceanogr.,* 2000, vol. 45, pp. 569–579.

10. Adl, S.M., Simpson, A.G.B., Farmer, M.A., Andersen, R.A., Anderson, O.R., Barta, J.R., Bowser, S.S., Brugerolle, G., Fensome, R.A., Fredericq, S., James, T.Y., Karpov, S., Kugrens, P., Krug, J., Lane, C.E., Lewis, L.A., Lodge, J., Lynn, D.H., Mann, D.G., McCourt, R.M., and Mendoza, L., Moestrup, Ø., Mozley-Standridge, S.E., Nerad, T.E., Shearer, C.A., Smirnov, A.V., Spiegel, F.W., and Taylor, M.F., Jr., The New Higher Level Classification of Eukaryotes with Emphasis on the Taxonomy of Protists, *J. Eukaryot. Microbiol.,* 2005, vol. 52, pp. 39–4519.

11. Vincent, W.F., Cyanobacterial Dominance in the Polar Regions, in *The Ecology of Cyanobacteria*, Whitton, B.A. and Potts, M., Eds., Dordrecht: Kluwer Academic, 2000, pp. 321–340.

12. Sherr, E.B., Sherr, B.F., Wheeler, P.A., and Thompson, K., Temporal and Spatial Variation in Stocks of Autotrophic and Heterotrophic Microbes in the Upper Water Column of the Central Arctic Ocean, *Deep-Sea Res.,* 2003, vol. 50, pp. 557–571.

13. Not, F., Massana, R., Latasa, M., Marie, D., Colson, C., and Eikrem, W., Pedrós-Alió, C., Vaulot, D., and Simon, N., Late Summer Community Composition and Abundance of Photosynthetic Picoeukaryotes in Norwegian and Barents Seas, *Limnol. Oceanogr.,* 2005, vol. 50, pp. 1677–1686.

14. Fogg, G.E., Some Comments on Picoplankton and Its Importance in the Pelagic Ecosystem, *Aquat. Microb. Ecol.*, 1995, vol. 9, pp. 33–39.

15. Booth, B.C. and Horner, R.A., Microalgae on the Arctic Ocean Section, 1994: Species Abundance and Biomass, *Deep-Sea Res.,* 1997, vol. 44, no. 2, pp. 1607–1622.

16. Schloss, I., Nozais, C., Mas, S., Hardenderg, van B., Carmack, E., Trembleay, J.-E., Brugel, S., and Demers, S., Picophytoplankton and Nanophytoplankton in the Southeastern Beaufort Sea (Mackenzie Shelf and Amundsen Gulf) during Fall 2002, *J. Mar. Syst.*, 2008, vol. 74, pp. 978–993.

17. Rokkan Iversen, K. and Seuthe, L., Seasonal Microbial Processes in a High-Latitude Fjord (Kongsfjorden, Svalbard): I. Heterotrophic Bacteria, Picoplankton and Nanofagellates, *Polar Biol.,* 2010. doi: 10.1007/s00300-010-0929-2

18. Li, W.K.W., Annual Average Abundance of Heterotrophic Bacteria and *Synechococcus* in Surface Ocean Waters, *Limnol. Oceanogr.,* 1998, vol. 43, pp. 1746–1753.

19. Ilyash, L.V., Zhitina, L.S., and Fedorov, V.D., *Fitoplankton Belogo morya* (Phytoplankton of the White Sea), Moscow: Yanus-K, 2003.

20. Boyd, P.W., Strzepek, R., Fu, F., and Hutchins, D.A., Environmental Control of Open-Ocean Phytoplankton Groups: Now and in the Future, *Limnol. Oceanogr.,* 2010, vol. 55, pp. 1353–1376.

21. Pantyulin, A.N., *Gidrologicheskie i ekologicheskie osobennosti Belogo morya. Geografiya, obshchestvo i okruzhayushchaya Sreda* (Hydrological and Ecological Characteristics of the White Sea. Geography, Society, and Environment), vol. 6, Dynamics and Interaction of the Atmosphere and Hydrosphere, Moscow: Gorodets, 2004, pp. 265–281.

22. Major Characteristics of Weather and Climate in the Northern Hemisphere in 2010. http://meteoinfo.ru

23. Sazhin, A.F., Rat'kova, T.N., and Kosobokova, K.N., Inhabitants of the White Sea Coastal Ice during the Early Spring Period, *Okeanologiya,* 2004, vol. 44, no. 1, pp. 82–89.

24. Li, W.K.W., McLaughlin, F.A., Lovejoy, C., and Carmack, E.C., Smallest Algae Thrive as the Arctic Ocean Freshens, *Science,* 2009, vol. 326, p. 539.