



Research article

Picophytoplankton distribution along Khatanga Bay-shelf-continental slope environment gradients in the western Laptev Sea

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ARTICLE INFO

Keywords:

Picophytoplankton
Picocyanobacteria
Chlorophyll *a*
Pico chlorophyll *a*
Laptev sea
Khatanga bay

ABSTRACT

The spatial variations of photosynthetic picoplankton abundance and biomass and the picoplankton's contribution to chlorophyll *a* concentration along the transect from Khatanga Bay to the continental slope in the western part of the Laptev Sea were studied in September 2017. Picoeukaryotes dominated in the picophytoplankton communities. Picophytoplankton in Khatanga Bay showed more variability than those over the Laptev shelf and continental slope: abundance and biomass were the highest in the southern part of the bay and markedly decreased with increasing salinity in its northern part. Picocyanobacteria were found over the shelf and slope at temperatures of +2.4 to -1.6°C and salinity from 22 to 34. Picophytoplankton contribution to total chlorophyll *a* on the shelf was higher than in Khatanga Bay. The study of picophytoplankton of Khatanga Bay and in the western Laptev Sea can serve as a baseline for future assessment of the Laptev Sea ecosystem response to interannual and climate changes.

1. Introduction

Picophytoplankton comprises two major groups, eukaryotic algae and cyanobacteria, and ranges in the size from 0.2 to 2.0 μm (or 3.0 μm) (Sieburth et al., 1978; Vaulot et al., 2008; Massana, 2011). Picoeukaryotes (PEs) are well adapted to harsh environment polar seas and in some areas numerically dominate arctic phytoplankton communities for most of the year (Sherr et al., 2003; Kiliyas et al., 2014). Picocyanobacteria (PC) are poorly represented in the Arctic seas in general (Murphy and Haugen 1985; Booth and Horner 1997; Mostajir et al., 2001; Sherr et al., 2003). Until recently, studies in the Arctic indicated the total absence of *Prochlorococcus*, and very limited presence of *Synechococcus* while the latter dominants in small size phytoplankton in most areas of the World Ocean (Li et al., 2009). However, recent research revealed the presence of *Synechococcus* in Arctic waters (Cottrell and Kirchman, 2012; Nelson et al., 2014; Paulsen et al., 2016) and the existence of *Synechococcus*, which was well adapted to the Arctic conditions and indigenous to high latitudinal ecosystems (Paulsen et al., 2016).

Previous research showed that small phytoplankton cells (<5 μm) accounted for up to 60%–90% of total chlorophyll *a* (Chl *a*) in areas with a long ice-coverage period and low primary production (Gosselin et al., 1997; Booth and Horner, 1997). Environmental conditions – temperature, salinity, nutrient concentrations and general light intensity strongly affect the picophytoplankton abundance (e.g., Metfies et al., 2016). However, factors that affected the spatial heterogeneity of picophytoplankton abundance at the mesoscale and submesoscale have not yet been sufficiently determined (Slapeta et al., 2006).

The pelagic environment of the epicontinental Arctic seas has changed significantly in recent decades. The changes were manifested in a reduction of ice cover in summer, decrease in ice thickness, increase in the ice-free period and to some extent the Arctic river discharge (Peterson et al., 2002; Macdonald et al., 2005). The increase of irradiance in the water column due to the reduction of Arctic sea ice may enhance primary production, mainly through the diatom response (Arrigo et al., 2012). However, this is only expected in areas with no nutrient limitation. Other studies predict a gradual shift of the Arctic phytoplankton community toward small-sized algae in nutrient limited surface waters (Moran et al.,

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2010), which may affect ecosystem productivity and carbon flux in the Arctic Ocean. Thus, estimates of picophytoplankton biomass and its contribution to the total phytoplankton under different environmental conditions are critical for better understanding of the Arctic pelagic ecosystem response to ongoing climate changes. All of the above determine the importance of assessing the distribution of picophytoplankton along pronounced thermohaline gradients, for example, along the estuary-shelf-continental slope gradient, to understand possible ecosystem trends with climate change.

The Laptev Sea ranks second among the Arctic seas (after the Kara Sea) by volume of riverine discharge (Gordeev, 2012). The western and eastern parts of the Laptev Sea differ significantly in hydrological and hydrophysical conditions (Dmitrenko et al., 2012; Bauch et al., 2014). While the eastern part of the basin is affected by Lena River inflow (525 km³/year) its western part is affected by much smaller freshwater discharge of the Khatanga River (85 km³/year), which flows through the long (>200 km) Khatanga Bay. The western part of the Laptev Sea is characterized by the later melt of seasonal sea ice (Karklin and Karelin, 2009). The picophytoplankton in the Lena River delta were studied in early September 1991 (Moreira-Turcq and Martin, 1998; Heiskanen and Keck, 1996) and no data are currently available for the Khatanga River delta.

The objectives of this study were: (1) to estimate picophytoplankton abundance and biomass and their variability in relation to pronounced environmental changes along the transect from the inner part of Khatanga Bay to the shelf slope in the western part of the Laptev Sea in early fall and (2) to estimate the contribution of picophytoplankton to the total Chl *a* in different environmental conditions.

2. Materials and methods

2.1. Sample collection and processing

The samples were collected during the 69th cruise of R/V Akademik Mstislav Keldysh along the 640-km-long transect that has the latitudinal range 73° 28.4' to 78° 03.0'N (Figure 1). Observations were conducted on 17–20 September 2017. Eleven transect stations were located in the following oceanographic domains: Khatanga Bay (stations 5627–5631), the shelf (stations 5632–5634, 5590_2, 5591_2), and the continental slope (station 5635).

The vertical distributions of temperature, salinity and Chl *a* fluorescence were estimated at every station using a CTD probe SBE-911 Plus. Salinity was measured using the Practical Salinity Scale. The vertical extent of the upper mixed layer (Z_m) was defined as the depth where the vertical sigma-t gradient reached 0.03 kg m⁻³ (de Boyer Montégut et al., 2004; Tremblay et al., 2009). The intensity of surface irradiance measured using a LI-190SA (LI-COR) sensor was used to estimate the depth of the euphotic zone (Z_{eu} , 1% of surface irradiance). In the absence of underwater hydrooptical measurements, the diffuse attenuation coefficient for downwelling solar radiation in the visible spectrum (K_d) was calculated according to Demidov et al. (2017).

Water samples for picoplankton assessment and measurements of Chl *a* and nutrient concentrations were collected using 5-l Niskin bottles of the Sea-Bird Electronics SBE-32 sampling system. From three to five depths were sampled at each station, including the upper mixed layer, the fluorescence maximum, and the layer below the pycnocline (Table 1).

2.2. Picophytoplankton enumeration

We used flow cytometry (BD Accuri C6, USA) and epifluorescence microscopy (Leica DM1000, Switzerland) to enumerate picophytoplankton. Both methods were used directly on board of the research vessel. According to a previous study (Ribeiro et al., 2016) BD Accuri C6 gives adequate results in counting photosynthetic eukaryotes but not cyanobacteria. Epifluorescence microscopy was used to count photosynthetic prokaryotes.

2.2.1. Flowcytometric analysis of picophytoplankton

The sub-samples (3.6 mL) were pre-filtered through a 20- μ m nylon gas and immediately analyzed using a flow cytometer (BD Accuri C6) equipped with 488- and 640-nm laser sources. Forward angle light scatter, right angle light scatter, orange fluorescence from phycoerythrin (575 \pm 20 nm) and red fluorescence from chlorophyll (675 \pm 10 nm) were measured. Microspheres (1 μ m, Fluoresbrite plain YG, Polysciences) were added to each sample as an internal standard. The average coefficient of variation for duplicate sample counting was 5.7%.

2.2.2. Epifluorescence microscopy analysis of picophytoplankton

The sub-samples (10 mL) were placed in a filtration funnel and incubated for 5–7 min after the saturated solution of primulin was added.

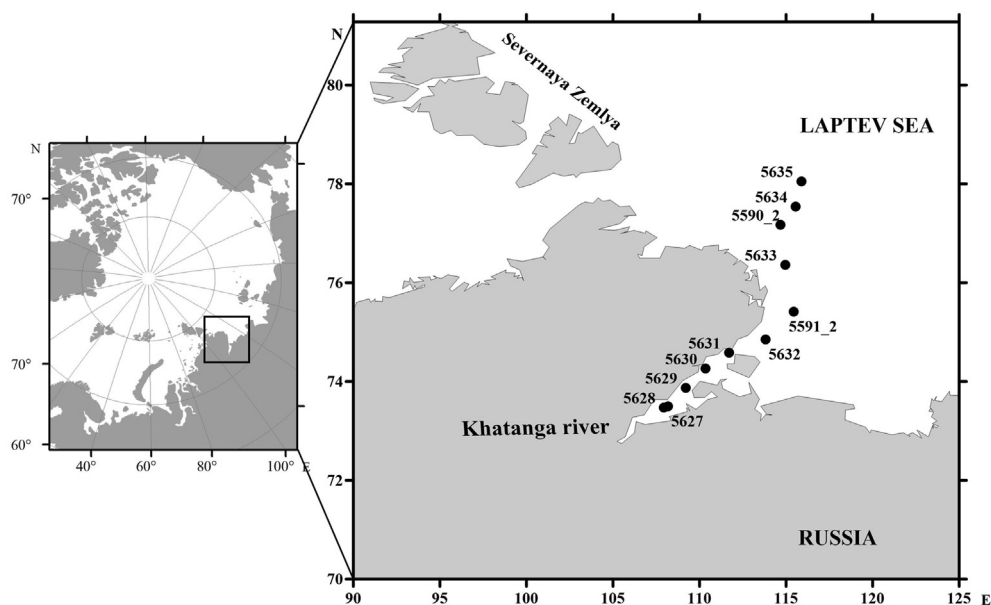


Figure 1. Sampling stations in the western part of the Laptev Sea.

Table 1. Station depth (H, m), sampling depth (D, m), euphotic layer depth (Z_{eu} , m), upper mixed layer depth (Z_m , m), surface temperature (T_o , °C) and salinity (S_o), and abundance of picocyanobacteria on sampling depths ($N_{PC} \times 10^9$ cells m^{-3}).

станция	H	D	Z_{eu}	Z_m	T_o	S_o	N_{PC}
5628	12	0; 4; 8	10	4	3.62	3.51	1.25; 0.49; 0.98
5627	15	0; 5; 12	10	2	3.62	3.50	1.16; 1.20; 0.71
5629	21	0; 12	12	2	3.34	11.18	0.22; 0.13
5630	26	0; 14; 20	13	2	2.3	17.14	0.31; 0.07; 0
5631	29	0; 10; 18	7	7	2.53	18.88	0; 0; 0
5632	34	0; 10; 17	18	10	2.16	21.89	0.11; 0; 0.04
5591_2	44	0; 13; 24	23	5	2.31	22.34	0; 0; 0
5633	44	0; 10; 18	30	6	1.52	27.91	0.02; 0.67; 0.02
5590_2	63	0; 13; 24	23	8	0.66	31.61	0; 0.02; 0
5634	186	0; 22; 40	24	14	-0.39	30.00	0; 0; 0.02
5635	857	0; 27; 45	23	17	-1.33	32.33	0; 0.02; 0

Each sample was preserved with glutaraldehyde at a final concentration of 1%. Nuclear filters (0.12- μ m pore diameter, Dubna, Russia) prestained with Sudan black were used for filtration. The cells on the filter were counted under a Leica DM1000 epifluorescence microscope at $\times 100 \times 10 \times 1.3$ magnification. Depending on cell concentration, 30 to 50 fields were examined and the cell size was measured. The “type” of fluorescence was also determined: spherical cells with a diameter ≤ 1.5 μ m with orange fluorescence from phycoerythrin (575 \pm 20 nm) were considered to be picocyanobacteria. Orange fluorescence under the blue excitation was also peculiar to Cryptophytes, but the latter can be easily identified by their asymmetric cell shape and were absent in our samples. Cell volume was converted to carbon using different conversion factors. For prokaryotes which cell-sizes varied from 0.8 to 1.2 μ m (average 1 μ m) conversion factor of 470 fg C/cell was used (Verity et al., 1992). The carbon biomass of picoeukaryotes was estimated according to a conversion factor of $\log C = 0.9411 \log V - 0.60$ (DuRand et al., 2001).

2.3. Chl *a* measurement

Chl *a* concentrations were determined using the fluorometric method (Holm-Hansen et al., 1965). To determine total Chl *a*, seawater samples (500 mL) were filtered over Whatman GF/F glass fiber filters under low vacuum (~ 0.3 atm) and then extracted in 90 % acetone at 5 °C in the dark for 24 h. The fluorescence of the extracts was measured using a fluorometer (Trilogy, Turner Designs) before and after acidification with 1 N HCl. The fluorometer was calibrated before and after the cruise using pure Chl *a* (Sigma) as a standard. Chl *a* concentration was calculated according to Holm-Hansen and Riemann (1978).

To determine the picofraction Chl *a* (pico Chl *a*) concentration, 1000-ml water samples were prefiltered by gentle reverse filtration through nuclear filters with 3- μ m pores (Dubna, Russia). The resulting filtrate was processed as described above.

Chl *a* concentration, picophytoplankton abundance and biomass were integrated over the euphotic zone and surface mixed layer using the trapezoidal method (Knap et al., 1996), and were averaged over the euphotic zone and upper mixed layer for every station.

2.4. Evaluation of nutrient concentration

Samples for nutrient evaluation were taken from corresponding Niskin bottles and treated immediately after sampling without preservation. In the area with a high particulate organic matter concentration (Khatanga Bay), water samples were prefiltered through a 1- μ m nuclear pore filter (Dubna, Russia). P- PO_4 , N- NO_3 , N- NO_2 , N- NH_4 , and Si(OH) $_4$ concentrations were assessed according to Grasshoff et al. (1999). Nitrates were reduced to nitrites using a standard cadmium column. N- NO_2 concentration was measured using the Bendschneider and Robinson method. For N- NH_4 concentration measurements, a modified Solorzano method was used. P- PO_4 concentration was estimated using the Murphy

and Riley method. Silicate was determined using the Strickland and Parsons method. Colorimetric measurements were performed using HACH Lange DR 2800 and LEKI SS2107UV spectrophotometers.

2.5. Statistical analysis

We used Spearman's correlation assay to determine the general relationships. Multivariate analysis (canonical correspondence analysis, CCA) was conducted using PAST 3.10 to estimate the influence of environmental factors on biomass of PC and PE, pico Chl *a* and total Chl *a* (Hammer et al., 2001). Differences in the picophytoplankton abundance and biomass values between stations and depths were assessed using one-way analysis of variance (ANOVA).

3. Results

3.1. Environmental parameters, nutrients and total Chl *a*

Our studies covered three distinct oceanographic areas: Khatanga Bay, the Laptev Sea shelf and the continental slope. Hydrophysical and hydrochemical conditions over the investigated area exhibited high level of spatial latitudinal variability (Figure 2). In Khatanga Bay, the surface salinity was lower and temperature was higher than above the shelf (Table 1, Figure 2). The upper mixed layer ranged from 2 to 7 m in the bay, 5–14 m on shelf, and was 17 m over the continental slope. The depth of the euphotic zone exceeded the upper mixed layer and was found at depths of 7–10 m in Khatanga Bay, 16–21 m on the shelf, and to 26 m over the continental slope (Table 1).

Nutrient concentrations in the upper mixed layer of Khatanga Bay were generally higher than over the shelf (Figure 2). The highest values were found in the southern part of the bay (stations 5627–5628) and the lowest on the northernmost station (5634) on the outer shelf and over the continental slope (station 5635). The nutrient concentrations in the shelf and slope areas generally markedly increased below the pycnocline. An exception was found at shelf station 5634, where nutrient concentration in the layer of subsurface chlorophyll maximum (SCM) at depths of 18–24 m were the same as in the surface layer. The (NO $_3$ +NO $_2$):PO $_4$ molar ratio on different depths ranged from 0.1 to 10 in Khatanga Bay, from 0.2 to 9 in the shelf area, and from 3.4 to 14.5 over the continental slope. These values were lower than the 16:1 Redfield value (Redfield et al., 1963), suggesting that dissolved inorganic nitrogen was the macronutrient in lowest supply for phytoplankton growth throughout the entire transect. Nitrogen limitation is common in Arctic shelf seas such as Baffin Bay (Ardyna et al., 2011; Garneau et al., 2007; Tremblay et al., 2009) and Hudson Bay (Ferland et al., 2011; Lapoussi re et al., 2013).

Total Chl *a* concentration in the surface layer varied from 0.2 to 1.7 mg m^{-3} along the transect (Figure 3). Average total Chl *a* concentration in surface layer of Khatanga Bay (1.3 mg m^{-3}) exceed values measured over the shelf (0.3 mg m^{-3}) by more than four times. Mean values of

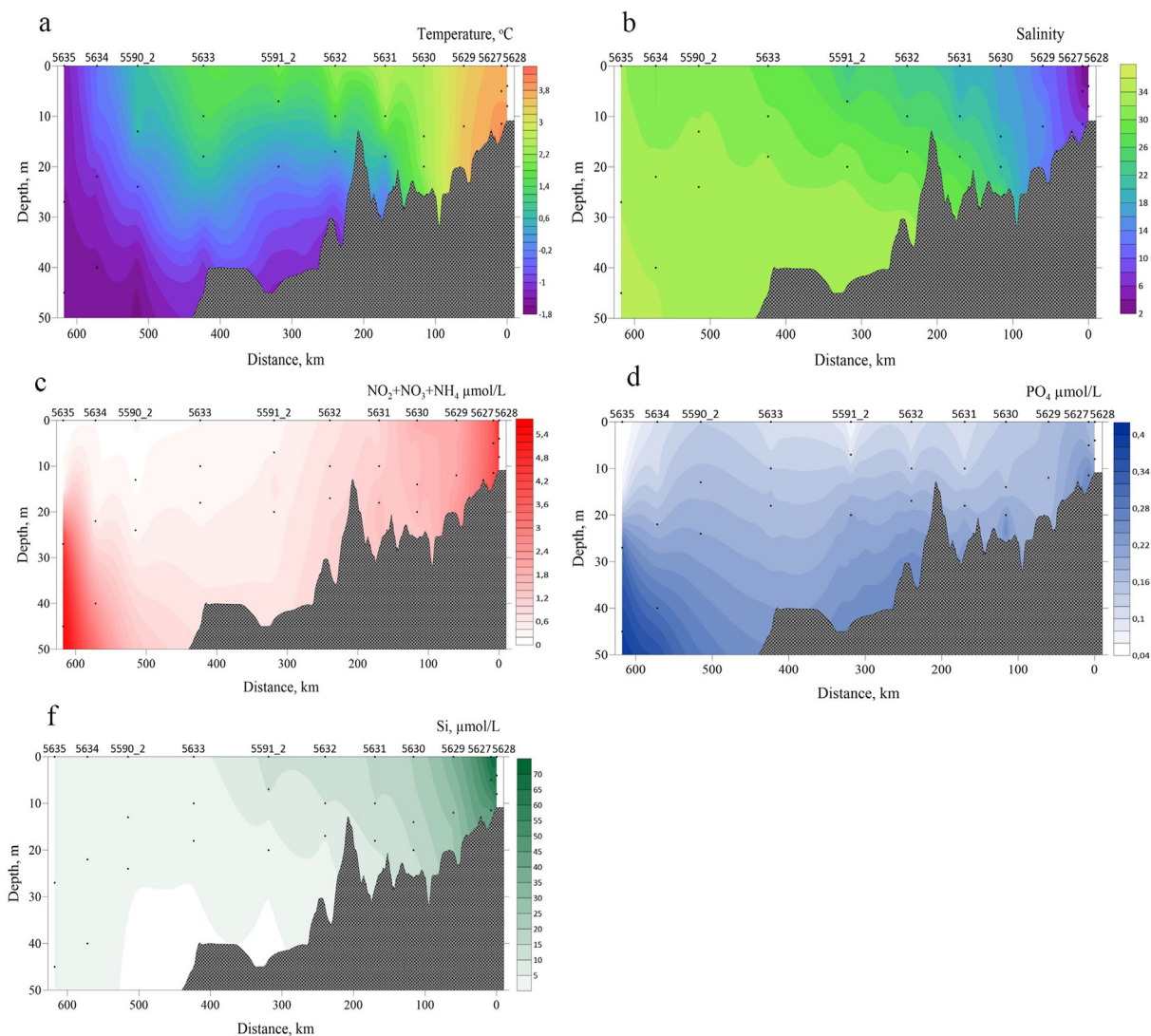


Figure 2. Environmental profiles of sampling locations showing temperature (a), salinity (b), concentrations of total inorganic nitrogen ($\text{NO}_2 + \text{NO}_3 + \text{NH}_4$, $\mu\text{mol L}^{-1}$) (c), phosphorus (PO_4 , $\mu\text{mol L}^{-1}$) (d), and silicon (Si, $\mu\text{mol L}^{-1}$) (f). Black dots: sampling depths.

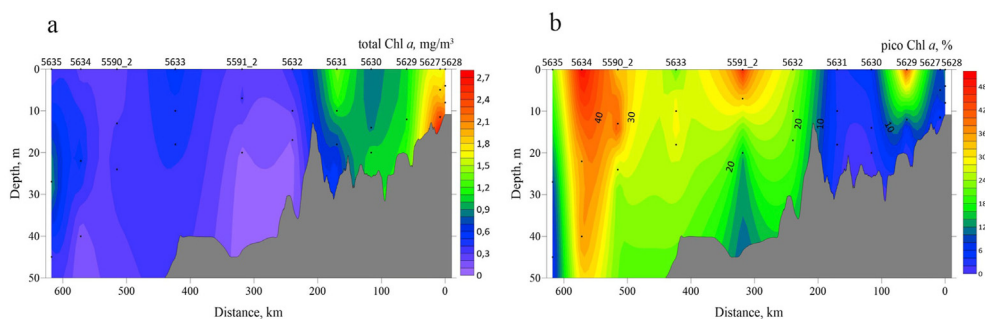


Figure 3. Distribution of total chlorophyll a (total Chl a) (according to Demidov et al., 2020) (a) and relative contribution of pico chlorophyll a (pico Chl a, %) (b) in the transect. Black dots: sampling depths.

total Chl a concentrations in the euphotic zone and in the upper mixed layer were also significantly higher in the bay (1.29 and 1.25 mg m^{-3} , respectively) than on the shelf (0.29 and 0.36 mg m^{-3}). Because the depths of the euphotic zone and the upper mixed layer in Khatanga Bay were markedly lower than on the shelf, the average integral total Chl a concentrations under 1 m^2 in the layers were similar in both domains.

3.2. Picophytoplankton abundance, biomass and Chl a concentration

The pico-fraction of phytoplankton comprised cyanobacteria and eukaryotic algae. The abundance of cyanobacteria exhibited markedly uneven distribution along the transect. The highest abundance of PC in the upper mixed layer ($1.18 \times 10^9 \text{ cells m}^{-3}$) was indicated in the southern part of Khatanga Bay and it gradually decreased northwards to

zero values by station 5631 at the inner part of the shelf (Table 1). Further over the shelf, the PC abundance varied from 0 to 0.67×10^9 cells m^{-3} at different sampling depths. Over the continental slope, cyanobacteria were found only at 27 m depth at a relatively low abundance of 0.02×10^9 cells m^{-3} .

Picophytoplankton abundance, biomass and pico Chl *a* in the surface layer ranged from 1.7 to 19×10^9 cells m^{-3} , from 0.54 to 4.87 mg C m^{-3} , and from 0.05 to 0.47 mg m^{-3} respectively (Table 2). The highest values were found in warmer and freshened waters in the southern part of Khatanga Bay. The average picophytoplankton abundance in the surface layer in the bay was significantly higher than on shelf while the average biomass and Chl *a* did not differ statistically (Table 2). The average picophytoplankton abundance, biomass and Chl *a* (m^3) in the euphotic zone and upper mixed layer did not vary significantly in the area from Khatanga Bay to the outer part of the shelf. Because the depths of the layers were greater on the shelf than in the bay, picophytoplankton average integral abundance, biomass, and Chl *a* concentration (under 1 m^2) were higher on the shelf than in the bay.

PEs were the main contributors to the total picophytoplankton abundance and biomass. PC input to the total picophytoplankton biomass in Khatanga Bay did not exceed 26% in the surface layer and 16% in upper mixed layer and the euphotic layer. PC contribution to picophytoplankton biomass over the shelf and continental slope was lower than 13% and 1%, respectively.

3.3. Picophytoplankton contribution to total Chl *a*

The contribution of picophytoplankton to the total Chl *a* in Khatanga Bay decreased from its southern part seaward (Figure 3). This pattern was well pronounced in the surface layer (from 12% to 3%), euphotic layer (from 10% to 3%), and upper mixed layer (from 12% to 3%). The contribution of picophytoplankton to the total Chl *a* on the shelf was significantly higher and varied from 21% to 50% in the surface layer, from 15% to 40% in the euphotic layer and from 25% to 39% in the upper mixed layer. Over the continental slope, the contribution of picophytoplankton to total Chl *a* made up 23% in the surface layer, and by 13% in upper mixed layer and the euphotic layer.

3.4. Vertical distribution

The vertical distribution of picophytoplankton biomass, pico Chl *a* and its contribution to the total Chl *a* significantly varied from station to station along the transect. The SCM was found under the pycnocline over the continental slope (station 5635) and in the adjacent area of the outer part of the shelf (station 5634). The maximum was located at the depths of 22–27 m at water temperatures $< -1^\circ C$. Total Chl *a* concentration in

the SCM at stations 5634 and 5635 ($0.57 \text{ mg } m^{-3}$ and $0.97 \text{ mg } m^{-3}$ respectively) was 2–3 times higher than in the surface layer ($0.24 \text{ mg } m^{-3}$ and $0.30 \text{ mg } m^{-3}$). Pico Chl *a* was also slightly higher in the SCM but its contribution to total Chl *a* at stations 5634 and 5635 (34% and 8%, respectively) was lower than in the surface layer (50% and 23%, respectively). Picophytoplankton biomass in the subsurface maximum was the same as in the surface layer. Notably, inorganic nitrogen and phosphorus concentrations increased compare with the surface only over the continental slope (Figure 2). The N/P ratio increased from 3.6 in the surface layer to 15.3 at the depth of the SCM at station 5635. However, at the northernmost station of the outer part of the shelf (station 5634), nutrient concentrations and N/P ratio at SCM were low and did not differ from those in the surface layer.

3.5. Picophytoplankton biomass and environmental factors

CCA analysis showed that level of picophytoplankton biomass was associated with certain environmental factors (Figure 4). The first canonical axis alone explained 85.9% of the variance. The PC biomass and total Chl *a* concentration positively correlate with the presence of warm riverine water, high levels of silica and total nitrogen. Contrary to PC the PE biomass, total picoplankton biomass and pico Chl *a* were associated with low water temperature, high salinity, and phosphate concentrations. The second canonical axis explained 14.0% of variance and was less informative.

PC biomass positively correlated with water temperature ($r_s = 0.78$, $p < 0.001$), dissolved inorganic nitrogen ($r_s = 0.6$, $p < 0.001$), phosphates ($r_s = 0.54$, $p < 0.001$), and silica ($r_s = 0.67$, $p < 0.001$), and negatively correlated with salinity ($r_s = 0.67$, $p < 0.001$).

4. Discussion

In our study, we present the first data on the abundance and biomass of photosynthetic picoplankton and its contribution to the total phytoplankton in terms of Chl *a* in the western part of the Laptev Sea. The parameters were examined over a background of markedly changing environmental conditions from the southern part of Khatanga Bay to the continental slope area in the north. Picophytoplankton in Khatanga Bay was characterized by the most pronounced spatial variability. The decrease of riverine water impact from the southern to the northern parts of the bay and respective increase in salinity and decreases in temperature and nutrient concentration were the main factors that determined latitudinal picophytoplankton changes. In the investigated area, picophytoplankton abundance and biomass sharply decreased northward in compliance with the decrease of riverine water impact. These changes agree with the data showing higher abundance of picoalgae in river

Table 2. Picophytoplankton abundance N ($\times 10^9$ cells m^{-3}), biomass B (mg C m^{-3}), total chlorophyll *a* (total Chl *a*, mg m^{-3}), pico chlorophyll *a* (pico Chl *a*, mg m^{-3}) and contribution of pico Chl *a* (%) to the total Chl *a* in surface, euphotic and upper mixed layers in Khatanga Bay (stations 5627–5631), over the shelf (stations 5632–5634, 5590_2, 5591_2) and continental slope (station 5635).

Station	surface layer					euphotic layer					upper mixed layer				
	N	B	total Chl <i>a</i>	pico Chl <i>a</i>	%	N	B	total Chl <i>a</i>	pico Chl <i>a</i>	%	N	B	total Chl <i>a</i>	pico Chl <i>a</i>	%
5628	19.03	4.87	1.72	0.20	12	17.55	3.71	2.26	0.23	10	17.95	4.03	1.80	0.21	12
5627	18.92	3.74	1.64	0.12	7	17.18	3.42	1.82	0.13	7	18.48	3.67	1.54	0.14	9
5629	3.35	0.67	1.06	0.08	7	2.68	0.53	1.07	0.07	7	2.68	0.53	1.07	0.07	7
5630	2.59	0.56	0.81	0.05	6	2.04	0.73	0.81	0.04	5	2.04	0.73	0.81	0.04	5
5631	1.72	0.54	1.4	0.04	3	2.44	0.58	1.27	0.04	3	2.44	0.58	1.27	0.04	3
5632	4.28	1.54	0.43	0.11	26	2.91	1.15	0.27	0.04	15	3.56	1.38	0.32	0.08	25
5591_2	5.33	1.78	0.26	0.12	46	3.56	1.34	0.26	0.09	35	5.04	1.81	0.30	0.11	37
5633	3.44	0.87	0.57	0.12	21	2.56	0.75	0.37	0.10	27	4.33	1.21	0.52	0.13	25
5590_2	6.78	2.05	0.23	0.07	30	5.56	1.61	0.29	0.10	34	7.02	2.02	0.27	0.10	37
5634	8.52	1.96	0.24	0.12	50	7.92	1.94	0.40	0.16	40	8.83	2.10	0.41	0.16	39
5635	2.45	0.77	0.30	0.07	23	1.66	0.74	0.63	0.08	13	1.80	0.78	0.63	0.08	13

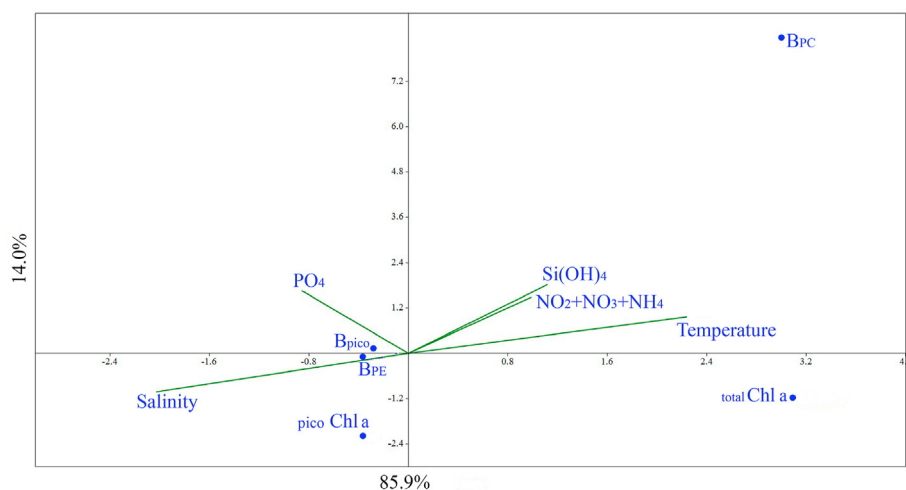


Figure 4. Canonical correspondence analysis (CCA) showing the relationships between PE biomass (B_{PE}), PC biomass (B_{PC}), pico chlorophyll *a* (pico Chl *a*), total chlorophyll *a* (total Chl *a*) and environmental factors (temperature (T), salinity (S), total inorganic nitrogen (nitrite, nitrate and ammonium N), phosphates (PO_4) and silica ($Si(OH)_4$) in Khatanga Bay, over the shelf and continental slope.

waters compared with marine ones (Bell and Kalff, 2001; Contant and Pick 2013). Similar results were obtained in the Lena River delta (Moreira-Turcq and Martin, 1998), where picoplankton abundance decreased with increasing salinity. Our assessments of picophytoplankton abundance and biomass in Khatanga Bay were lower than those revealed in the eastern part of the Laptev Sea in September 1998 (Moreira-Turcq and Martin, 1998). In the Lena River delta and over the adjacent shelf, picophytoplankton abundance in the surface layer varied from 5 to 54×10^9 cells m^{-3} , biomass in a range of 6–56 mg C m^{-3} . The greatest picophytoplankton abundance with the predominance of *Synechococcus* was revealed in the delta of the Lena River at a salinity of 3.17 (Moreira-Turcq and Martin, 1998). The authors suggest that the high biomass was related to the supply of nutrients by Lena River enriched waters during the summer-autumn period (Cauwet and Sidorov, 1996).

We found that the range of variability of picophytoplankton abundance over the shelf and the continental slope in the western part of the Laptev Sea significantly was lower than that observed in Khatanga Bay. The coefficient of variation of picophytoplankton abundance in the euphotic layer in the bay was 101% but was only 56% on the shelf and in the continental slope area. This difference is due to more variable environmental conditions in the bay because of the active interaction of fresh and marine water.

4.1. Distribution of cyanobacteria in relation to the environment gradients

The decrease of PC abundance was well exhibited from the southern part of Khatanga Bay to the continental slope. *Synechococcus* was highly abundant in the southern part of the bay, was not found in its northern part, and appeared in very low numbers over the shelf. Such a distribution pattern and negative correlation of *Synechococcus* abundance and salinity suggest that PC in the bay were mainly represented by freshwater forms of *Synechococcus* with a narrow range of salinity tolerance. *Synechococcus* is often found in Arctic lakes and rivers, and freshwater runoff is considered as a source of *Synechococcus* cells to the Arctic Ocean (Vincent, 2000). Similar observations were made in the Beaufort Sea and in Labrador fjords, where cyanobacteria distribution was also associated with freshwater input (Blais et al., 2012; Waleron et al., 2007; Simo-Matchima et al., 2016). The cyanobacteria abundance in Khatanga Bay was an order of magnitude lower than in the Lena River delta (Moreira-Turcq et al., 2001). This may be due to the higher abundance of *Synechococcus* related to the higher fresh water inflow to the Lena delta compared with Khatanga Bay.

Different *Synechococcus* genotypes that occupy different ecological niches have been identified in natural environments. For example, more than seven *Synechococcus* genotypes were revealed in Chesapeake Bay, two of which could withstand significant fluctuations in salinity (Chen et al., 2006). We suppose that genotypes tolerant to salinity changes do not exist in Khatanga Bay because of intensive tides and low water retention time in the bay. Obligate marine *Synechococcus* has low tolerance to salinity changes (Waterbury et al., 1986) and thus does not survive in the freshened water of Khatanga Bay. They reappear in relatively saline water of the outer part of the shelf and continental slope.

Over the western Laptev shelf, PC were revealed at different depths at a temperature from 2.4°C to -1.6°C and salinity from 22 to 34. Cyanobacteria abundance in the shelf area was much lower than that in Khatanga Bay and varied from 0 to 0.67×10^9 cells m^{-3} . Over the continental slope, cyanobacteria were found only at 27 m depth with abundance of 0.02×10^9 cells m^{-3} . According to previous observations *Synechococcus* was found in low numbers at low temperatures such as $<4^\circ\text{C}$ (<0.1 cells $\times 10^9$ cells m^{-3} ; Waterbury et al., 1986) and $<2^\circ\text{C}$ (Shapiro and Haugen, 1988; Gradinger and Lenz, 1995). However, even until recently, *Synechococcus* was considered to be absent in Arctic Ocean (Pedrós-Alió et al., 2015) in contrast to cold adapted eukaryotic picophytoplankton which high abundance was observed in the Arctic (Sherr et al., 2003; Lovejoy et al., 2007; Tremblay et al., 2009; Zhang et al., 2015). In the western Canadian Arctic, Cottrell and Kirchman (2012) found *Synechococcus* abundances of 40–80 cells/mL (0.04 – 0.08×10^9 cells m^{-3}) in coastal waters of the Chukchi and Beaufort Seas at 71.5°N during both summer and winter cruises. Past studies showed that *Synechococcus* could grow in the Arctic at temperatures near the freezing point for marine water (-1.8°C) (Nelson et al., 2014). Paulsen and co-authors encountered high *Synechococcus* abundance up to 21,000 cells/mL (21×10^9 cells m^{-3}) at 79°N and documented its presence as far north as 82.5°N in the Atlantic water inflow to the Arctic Ocean (Paulsen et al., 2016). Abundance above 1000 cells/mL (10^9 cells m^{-3}) was observed in water colder than 2°C at several distinct stations. Our estimates of *Synechococcus* abundance in the area north of 72°N correspond to these values. *Synechococcus* abundance reached 669 cells/mL (0.67×10^9 cells m^{-3}) at the station 5633 at 10 m depth where temperature and salinity were -0.4°C and 33, respectively. Cyanobacteria abundance in the Laptev shelf corresponded to that revealed in the Beaufort Sea (Tremblay et al., 2009). Cyanobacteria were found at an abundance of 22 cell/mL (0.02×10^9 cells m^{-3}) in the SCM above the continental slope (station 5635) at temperature -1.4°C and salinity 33.

Over the outer part of the shelf and the continental slope, *Synechococcus* at 22 cells/ml (0.02×10^9 cells m^{-3}) was found below the euphotic layer at depths down to 40 m. *Synechococcus* can grow in very low light and darkness (Paulsen et al., 2016). The ability of *Synechococcus* to grow in very low light is presumably coupled to its capacity to consume dissolved organic matter (Palenik et al., 2003; Cottrell and Kirchman, 2009). Yelton et al. (2016) indeed found that the genetic potential for mixotrophy in picocyanobacteria (through osmotrophy) is globally distributed.

4.2. Distribution of picoeukaryotes in relation to the environment gradients

The distribution of PEs was similar to that of *Synechococcus*. PE abundance peaked in the southern part of Khatanga Bay. Similarly to *Synechococcus*, picoeukaryotes abundance markedly decreased in the upper mixed layer in the northern part of the bay. The exception was the northernmost station 5631 in the bay, where PC were absent and the PE abundance was slightly higher than at the more southern station 5630. We suppose that PEs like PC were mainly represented by freshwater forms in Khatanga Bay, and those on the shelf and above the continental slope by marine forms. The picoeukaryote abundance in Khatanga Bay was lower than in the Lena River delta – $1-19 \times 10^6$ cells/l vs. $1-40 \times 10^6$ cells/l ($1-19 \times 10^9$ cells m^{-3} vs. $1-40 \times 10^9$ cells m^{-3}) (Moreira-Turcq and Martin, 1998).

PE abundance in the surface layer and average abundance in the euphotic zone and upper mixed layer over the shelf and the continental slope did not differ significantly from those in Khatanga Bay. High picoeukaryote biomass was associated with low temperature high salinity waters. Within the Atlantic water inflow into the Arctic Ocean, PE abundance did not significantly correlate with any environmental parameters except for temperature (Paulsen et al., 2016). The picoeukaryote abundance we observed over the shelf and the continental slope in the western part of the Laptev Sea was close to that in the Canadian basin and the Makarov basin (Booth and Horner, 1997) and in the southeastern Beaufort Sea ($4-9 \times 10^9$ cells m^{-3}) (Zhang et al., 2015).

Almost no data exist about the PEs taxonomic composition in the Laptev Sea. According to metagenomic analysis of the sample from only one station on the Laptev Sea shelf (Metfies et al., 2016) *Micromonas pusilla* clade Ea dominated in the photosynthetic picoeukaryote community. Haptophyta and Stramenopiles were also present.

4.3. Picophytoplankton in the subsurface chlorophyll maximum

The SCM was observed in areas with a stratified water column and nitrate-poor surface waters at the northernmost shelf station and above the continental slope. The SCM occurred in some ice-free Arctic waters during late summer and early fall (Martin et al., 2010; Arrigo et al., 2011; Ardyna et al., 2013; Brown et al., 2015; Demidov et al., 2018; Sukhanova et al., 2018). The SCM is located within the nutricline close to the lower boundary of the euphotic zone. At these depths, phytoplankton may find a compromise between favorable nutrient conditions and sufficient underwater irradiance. Above the continental slope, phosphate and nitrate concentrations were an order of magnitude greater at the depth SCM than in the surface layer.

Picophytoplankton biomass in the SCM exhibited similar values to the surface layer. The concentration of pico Chl *a* in the SCM at both sampling locations was higher than in the surface layer. At that the contribution of the picoplankton fraction to total Chl *a* was lower – on the outer shelf sampling location (station 5634) it decreased from 51% in the surface layer to 35% in the SCM; above the continental slope, the corresponding numbers were 23% and 8%. These characteristics agree with those observed in the south-west part of the Bering Sea, where in

April–May the picoplankton contribution to total Chl *a* ranged from 8% to 45% in the SCM (Stauffer et al., 2014).

4.4. Picophytoplankton contribution to total Chl *a*

Picophytoplankton contribution to total Chl *a* in the surface layer of Khatanga Bay (3–12%) was lower than in the Lena estuary (46–56%) (Heiskanen and Keck, 1996). Whereas we found that picophytoplankton contribution to the total Chl *a* on the western part of the Laptev Sea shelf (51%) and on the eastern part (62%) (Heiskanen and Keck, 1996) was close. The lower contribution of picophytoplankton to total Chl *a* in Khatanga Bay supports the conclusion that the share of picoplankton in total biomass is lower in areas under the influence of continental runoff (Metfies et al., 2016). Picophytoplankton contribution to total Chl *a* on the Laptev Sea shelf in September was 35% whereas in the Fram Strait and in the Central Arctic Ocean in June–September 2012 it comprised 60%–90% (Metfies et al., 2016). In the surface layer of southeastern Beaufort Sea, picophytoplankton share in total Chl *a* in summer 2010 was 44%–80% of (Zhang et al., 2015). In the oligotrophic waters of the Beaufort Sea the input of picoplankton in total Chl *a* in summer 2009 was 48%, and *Micromonas* sp. was determined to be the dominant form (Coupel et al., 2015).

5. Conclusions

We document here for the first time the abundance and biomass of photosynthetic picoplankton and its contribution to total Chl *a* in the western part of the Laptev Sea including Khatanga Bay and the continental slope area. Picoeukaryotes dominated everywhere in the picophytoplankton communities. The distribution of picophytoplankton in Khatanga Bay showed the maximal spatial variability, which was exhibited in decreasing abundance and biomass with increasing salinity. In light of these salinity changes, we suppose that picophytoplankton in the bay comprised mainly freshwater algae. On the eastern shelf of the Laptev Sea and over the continental slope, the picophytoplankton abundance varied less than in Khatanga Bay. Picocyanobacteria over the shelf and the continental slope exist at temperature from 2.3° to -1.6°C and salinity from 22 to 34. Picophytoplankton contribution to total phytoplankton Chl *a* on the shelf was higher than in Khatanga Bay. The SCM was found in two locations, over the outer shelf and over the continental slope, where contribution of pico Chl *a* to total Chl *a* was lower than in the surface layer.

Ongoing climate change may result in further freshening of the upper mixed layer of the Laptev Sea because of increased river discharge and precipitation (Zhang et al., 2013). The surface layer freshening will strengthen the halocline and further limit nutrient flux from deeper water columns. These processes promote the dominance of picophytoplankton in phytoplankton communities, which may consequently affect carbon cycles in the area. As it is the first to characterize of picophytoplankton abundance in the western Laptev Sea, our study gives a baseline for future assessment of the response of the Laptev Sea ecosystems to climate-induced processes.

Declarations

Author contribution statement

Tatiana A. Belevich: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Andrey B. Demidov: Performed the experiments; Analyzed and interpreted the data.

Peter N. Makkaveev, Sergei A. Shchuka: Contributed reagents, materials, analysis tools or data.

Mikhail V. Flint: Conceived and designed the experiments; Wrote the paper.

Funding statement

The expedition was supported by the Russian Foundation for Basic Research (project no. 18-05-60069 Arctic); hydrophysical data analysis was supported by Russian Foundation for Basic Research (project no. 18-05-60302 Arctic); the sample processing was supported by the Russian Foundation for Basic Research (project no. 19-05-00026a).

Data availability statement

Data included in article/supplementary material/referenced in article.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

Acknowledgements

We are grateful to the crew of the R/V Akademik Mstislav Keldysh and the participants of the 69 cruise of the R/V.

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