

UDC [582.261.1:551.326.7](265.54.04)

**SPECIES COMPOSITION OF THE MICROALGAL COMMUNITY
IN SEA ICE AND UNDER-ICE WATER
IN BAYS OF RUSSKY ISLAND (PETER THE GREAT BAY, SEA OF JAPAN)**

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Received 22.02.2024; revised 12.04.2024;
accepted 12.08.2025.

Sea ice can serve as a habitat for microalgae which can adapt to its unique conditions and successfully reproduce in it. This paper continues the analysis of material obtained for the first time from sea ice in two bays of Russky Island (the Sea of Japan) in 2020–2021 aimed at studying layer-by-layer distribution of the qualitative and quantitative composition of inhabiting microalgae. The taxonomic analysis allowed for identifying 87 species of microalgae from 48 genera and 7 divisions. The maximum species richness was characteristic of the Bacillariophyta division (57–100% of the species number in an ice layer). Algal flora of sea ice and under-ice water was formed mainly by benthic cosmopolites. The composition of dominant species varied depending on year, bay, and depth of an ice layer; the prevailing species were *Chaetoceros socialis* f. *radians*, *Cylindrotheca closterium*, *Navicula septentrionalis*, *Nitzschia frigida*, *Thalassiosira gravida*, *T. nordenskioeldii*, and *Plagioselmis* sp. Species composition varied most significantly between years of the study. Differences in species composition were also noted between bays and biotopes, as well as depending on the position of the layer in the ice column.

Keywords: ice algal flora, diatoms, Sea of Japan

Sea ice is a combination of rather harsh ecological factors. Nevertheless, some microalgae species are capable of adapting to this environment and successfully colonizing ice thereby affecting its physical and chemical properties. In turn, the state of ice, including its thickness and breakup timing, affects the ecosystem and the productivity of the entire water area during winter and early spring. Across this period, microalgae extensively developing within ice serve as a critical source of primary production.

Peter the Great Bay (the Sea of Japan) is one of the southernmost areas in the Northern Hemisphere capable of sustaining a stable ice cover for several months. However, research on its ice biota has been limited to the analysis of chlorophyll content and the value of primary production of microalgae [Kuznetsov, 1980], as well as production characteristics within ice of the Razdolnaya River estuary [Zvalinsky et al., 2010]. In the Voevoda and Novik bays of Russky Island, hydrological, hydrochemical, and ecological studies have been carried out [Barabanshchikov et al., 2015, 2018; Khristoforova et al., 2016, 2017; Mel'nichenko et al., 2014, 2017]. The sea-ice biotope in Peter the Great Bay has not been covered by algological surveys *prior* to this work, likely due to methodological challenges of sampling. In contrast,

the under-ice phytoplankton community in the bay has been extensively investigated in terms of species richness and abundance [Orlova et al., 2009; Ponomareva, 2017; Semkin et al., 2022; Shevchenko et al., 2020; Sorokin, Konovalova, 1973; Stonik, 2018].

The first research of sea-ice microalgae in two bays of Russky Island, the Voevoda and Novik bays, was conducted in 2020–2021, and the findings on the quantitative characteristics of ice microalgae were published [Yurikova, Begun, 2022]. This work is a continuation of the study, and its aim is to analyze microalgae species composition in both sea ice and under-ice water in the Voevoda and Novik bays of Russky Island during winter of 2020 and 2021.

MATERIAL AND METHODS

The study was carried out in February 2020 and 2021 in the Voevoda and Novik bays (Russky Island, the Sea of Japan) (Fig. 1). The environmental conditions during the field surveys and the sampling methodology were described in detail by E. Yurikova and A. Begun earlier [2022].

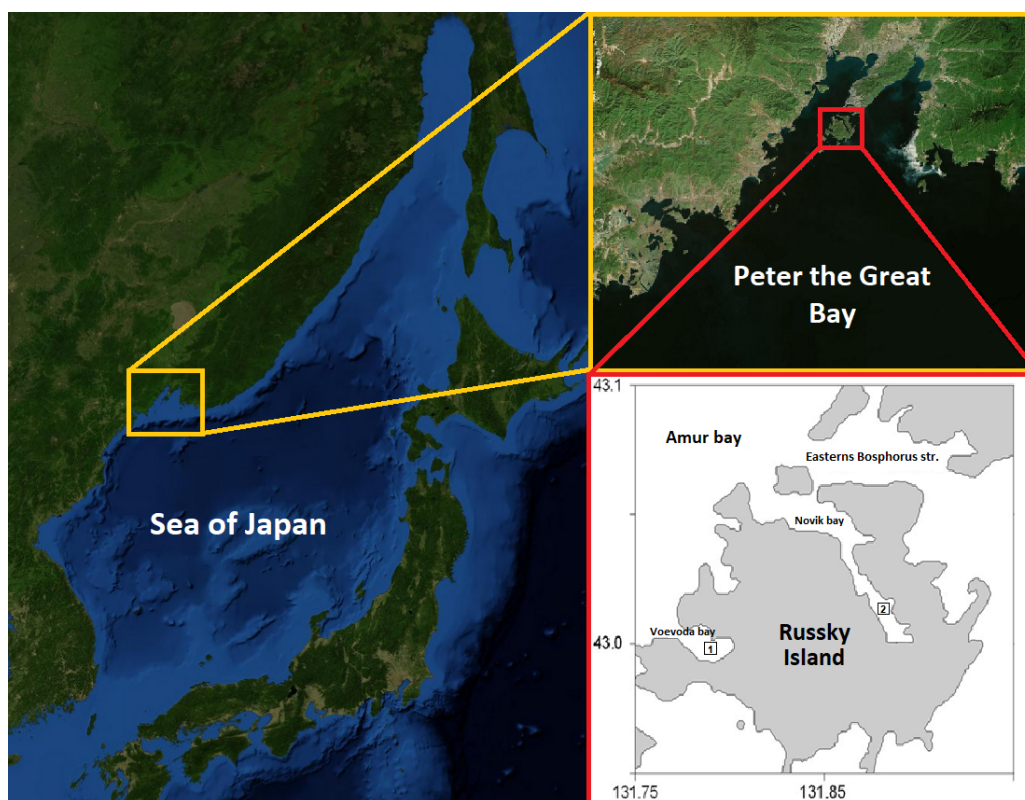


Fig. 1. Sampling sites in bays of Russky Island (the Sea of Japan): 1, the Voevoda Bay; 2, the Novik Bay

In 2020, ice thickness was approximately 40 cm in both bays; in 2021, it was about 60 cm. In 2020, 4 ice and 1 under-ice water samples were taken in each bay, while in 2021, 6 ice samples and 1 under-ice water sample were taken. Samples were fixed with Utermöhl's solution to a pale-yellow color [Utermöhl, 1958]. Following a method for sedimentation [Radchenko et al., 2010], after 12 days, the supernatant was decanted from each sample, and a residue of 100–200 mL was left.

For scanning electron microscopy, samples were prepared by boiling in 98% sulfuric acid for 40 min and then rinsed with distilled water. The material was analyzed in the laboratory of marine microbiota of NSCMB FEB RAS. For species identification of microalgae, we used a transmitted light

microscope Olympus BX41 equipped with a UPLanF1 100×/1.30 objective (Japan). Taxonomic identification was verified under a Zeiss Sigma 300 VP scanning electron microscope (the UK). Microalgal classification follows the system of [Konovalova et al., 1989] updated with nomenclatural revisions over the past 10 years. For identification, we used the guides [Hoppenrath et al., 2009; Identifying Marine Phytoplankton, 1997; Konovalova, 1998; Konovalova et al., 1989; Ryabushko, Begun, 2015].

Similarity analysis was performed in PRIMER v7.0.21 [Clarke, Gorley, 2015; Clarke, Warwick, 2001]. Non-metric multidimensional scaling was applied to ordinate algal communities based on species composition for different ice layers and under-ice water. The Sørensen coefficient was used as the distance measure.

RESULTS

In sea ice and under-ice water samples of 2020–2021, 87 taxa (species, varieties, and forms) from 48 genera and 7 divisions were identified (Table 1): Ochrophyta (2 species), Bacillariophyta (67), Cryptophyta (1), Dinophyta (13), Chlorophyta (2), Euglenophyta (1), and Haptophyta (1). Sixteen taxa could not be identified down to the species level. In ice, 79 species were recorded; out of them, 46 were exclusive to this biotope. In under-ice water, 41 species were registered, with only 8 being exclusive to it.

In 2020, 52 species from 31 genera and 4 divisions were noted for both bays, with 36 species out of them inhabiting the Voevoda Bay, and 37, the Novik Bay. Twenty-one species were common to two bays. In 2021, 63 species representing 41 genera and 7 divisions were found, with 50 species out of them inhabiting the Voevoda Bay, and 43, the Novik Bay. Thirty-one species were common for these two bays.

Ecological characteristic was determined for 66 out of 87 taxa revealed, and phytogeographical one, for 62. Benthic species dominated accounting for 50% (51% of recorded in sea ice, and 45% of registered in under-ice water). Benthic-planktonic species constituted 9%. Out of planktonic species, neritic ones accounted for 24%; oceanic for 8%; panthalassic for 8%; and freshwater for 1%. Phytogeographical analysis showed that cosmopolitans were the largest group comprising 40% of species (40% of noted in sea ice, and 48% of found in under-ice water). Out of the total number of species with known phytogeographic characteristic, tropical-arctic-boreal algae comprised 19%; tropical-boreal, 18%; arctic-boreal, 15%; boreal, 5%; and bipolar, 3%.

Table 1. Species composition of microalgae in sea ice (I) and under-ice water (UIW) of two bays of Russky Island in 2020–2021

Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
Ochrophyta										
<i>Ebria tripartita</i> (Schumann) Lemmermann, 1899	N	B	–	–	–	–	–	–	+	–
<i>Octactis speculum</i> (Ehrenberg) F. H. Chang, J. M. Grieve et J. E. Sutherland, 2017	O	C	+	–	+	–	+	–	+	–

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Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
Bacillariophyta										
<i>Actinoptychus senarius</i> (Ehrenberg) Ehrenberg, 1843	BP	C	–	–	–	–	+	–	–	–
<i>Amphora proteus</i> Gregory, 1857	Ben	C	–	–	–	–	+	–	–	–
<i>Asterionella formosa</i> Hassall, 1850	Fw	–	–	–	–	+	–	–	–	–
<i>Caloneis liber</i> (W. Smith) Cleve, 1894	Ben	C	–	–	–	–	–	–	–	+
<i>Chaetoceros socialis</i> f. <i>radians</i> (F. Schütt) A. I. Proshkina- Lavrenko, 1963	N	TAB	+	–	+	–	+	–	+	–
<i>Cocconeis costata</i> Gregory, 1855	Ben	C	–	–	–	–	+	–	+	–
<i>Cocconeis scutellum</i> Ehrenberg, 1838	Ben	C	+	–	–	–	+	+	+	–
<i>Coscinodiscus oculus-iridis</i> (Ehrenberg) Ehrenberg, 1840	P	AB	+	–	+	–	–	–	–	–
<i>Coscinodiscus</i> sp.	–	–	–	+	+	+	–	–	–	–
<i>Cyclotella</i> <i>choctawhatcheeana</i> Prasad, 1990	N	TB	–	–	+	–	+	–	–	–
<i>Cylindrotheca closterium</i> (Ehrenberg) Reimann et J. C. Lewin, 1964	BP	C	+	+	+	–	+	–	+	+
<i>Cymbella</i> <i>falsa diluviana</i> (Krasske) Lange-Bertalot et Metzeltin, 2009	Ben	B	–	–	–	–	+	–	–	–
<i>Detonula confervacea</i> (Cleve) Gran, 1896	N	AB	+	–	–	–	+	–	+	–
<i>Diploneis chersonensis</i> (Grunow) Cleve, 1894	Ben	TAB	–	–	+	–	–	–	–	–
<i>Diploneis lineata</i> (Donkin) Cleve, 1894	Ben	TB	+	–	–	–	+	–	+	–
<i>Diploneis smithii</i> (Brébisson) Cleve, 1894	Ben	C	–	–	–	+	+	–	–	–
<i>Entomoneis gigantea</i> var. <i>decussata</i> (Grunow) Nizamuddin, 1982	BP	B	–	–	–	–	+	–	+	+
<i>Grammatophora marina</i> (Lyngbye) Kützing, 1844	Ben	C	+	–	–	+	+	–	+	–

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Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
<i>Gyrosigma arcuatum</i> (Donkin) Sterrenburg, 2005	Ben	C	–	–	–	–	+	–	–	–
<i>Gyrosigma fasciola</i> (Ehrenberg) J. W. Griffith et Henfrey, 1856	Ben	–	–	–	–	–	+	–	–	–
<i>Gyrosigma tenuissimum</i> (W. Smith) Griffith et Henfrey, 1856	Ben	TB	–	–	–	–	–	–	+	–
<i>Halamphora costata</i> (W. Smith) Levkov, 2009	Ben	TB	+	–	–	–	+	–	+	–
<i>Halamphora cymbifera</i> (Gregory) Levkov, 2009	Ben	TB	+	–	–	–	+	–	–	–
<i>Haslea ostrearia</i> (Gaillon) Simonsen, 1974	Ben	TB	–	–	–	–	+	–	–	–
<i>Leptocylindrus minimus</i> Gran, 1915	N	TAB	+	–	–	–	–	–	–	–
<i>Licmophora abbreviata</i> C. Agardh, 1831	Ben	C	–	–	–	–	–	–	+	–
<i>Licmophora communis</i> (Heiberg) Grunow, 1881	Ben	AB	–	–	–	–	+	–	–	–
<i>Melosira moniliformis</i> (O. F. Müller) C. Agardh, 1824	BP	TAB	–	–	–	–	–	–	+	–
<i>Melosira moniliformis</i> var. <i>subglobosa</i> (Grunow) Hustedt, 1927	BP	AB	–	–	–	–	+	–	–	–
<i>Navicula distans</i> (W. Smith) Ralfs, 1861	Ben	TAB	–	–	–	–	+	+	–	+
<i>Navicula granii</i> (Jørgensen) Gran, 1908	N	AB	–	–	–	–	+	+	–	+
<i>Navicula johanrossii</i> Giffen, 1967	Ben	TB	–	–	–	–	+	–	–	–
<i>Navicula ramosissima</i> (C. Agardh) Cleve, 1895	Ben	TAB	–	–	–	–	+	+	–	+
<i>Navicula septentrionalis</i> Cleve, 1896	N	AB	+	+	–	–	+	–	+	+
<i>Navicula</i> sp. 1	–	–	+	+	+	+	–	–	–	–
<i>Navicula</i> sp. 2	–	–	+	–	–	–	–	–	–	–
<i>Navicula</i> sp. 3	–	–	–	–	–	–	+	–	–	–
<i>Navicula transitans</i> var. <i>derasa</i> (Grunow) Cleve, 1883	–	–	–	–	–	+	+	+	+	+

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Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
<i>Navicula transitans</i> var. <i>derasa</i> f. <i>delicatula</i> Heimdal, 1970	–	–	–	–	–	+	+	+	+	+
<i>Nitzschia angularis</i> W. Smith, 1853	Ben	C	–	–	–	+	–	–	–	–
<i>Nitzschia distans</i> W. Gregory, 1857	Ben	TB	–	–	+	–	–	–	–	–
<i>Nitzschia frigida</i> Grunow, 1880	–	–	+	+	+	+	+	–	+	+
<i>Nitzschia</i> sp. 1	–	–	–	–	–	–	+	–	–	–
<i>Nitzschia</i> sp. 2	–	–	–	+	+	+	–	–	–	–
<i>Nitzschia</i> sp. 3	–	–	–	–	–	+	–	–	–	–
<i>Nitzschia</i> sp. 4	–	–	–	–	–	–	+	+	+	+
<i>Odontella aurita</i> (Lyngbye) C. Agardh, 1832	BP	TAB	+	+	+	–	+	+	+	+
<i>Parlibellus delognei</i> (Van Heurck) E. J. Cox, 1988	Ben	C	–	–	–	–	+	+	–	+
<i>Pinnularia</i> sp.	–	–	–	–	–	–	+	–	–	–
<i>Pleurosigma elongatum</i> W. Smith, 1852	Ben	C	–	–	–	–	+	+	+	+
<i>Pleurosigma formosum</i> W. Smith, 1852	Ben	TAB	+	–	–	–	–	–	–	–
<i>Pleurosigma inflatum</i> Shadbolt, 1854	Ben	TB	+	+	–	–	–	–	–	–
<i>Pleurosigma intermedium</i> W. Smith, 1853	Ben	TAB	+	–	–	–	–	–	–	–
<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle, 1993	P	C	–	–	+	–	–	–	–	–
<i>Pseudo-nitzschia pungens</i> (Grunow ex Cleve) G. R. Hasle, 1993	P	C	–	–	+	–	–	–	–	–
<i>Rhaphoneis amphiceros</i> (Ehrenberg) Ehrenberg, 1844	Ben	TB	–	–	–	–	–	–	+	–
<i>Rhoicosphenia marina</i> (Kützing) M. Schmidt, 1889	Ben	TAB	–	–	–	–	+	–	–	–
<i>Skeletonema</i> sp.	–	–	+	–	+	–	+	–	–	–
<i>Tabularia fasciculata</i> (C. Agardh) D. M. Williams et Round, 1986	Ben	C	+	+	+	+	+	–	+	–

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Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
<i>Tabularia tabulata</i> (C. Agardh) Snoeijs, 1992	Ben	C	+	–	–	–	+	+	+	–
<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky, 1902	P	TAB	+	+	+	–	–	–	–	–
<i>Thalassiosira gravida</i> Cleve, 1896	P	Bip	–	–	–	+	+	–	–	–
<i>Thalassiosira nordenskiöldii</i> Cleve, 1873	N	AB	+	+	+	–	+	+	+	+
<i>Thalassiosira punctigera</i> (Castracane) Hasle, 1983	N	TB	–	–	–	–	+	+	+	–
<i>Thalassiosira</i> sp.	–	–	+	–	–	–	–	–	–	–
<i>Trachyneis aspera</i> (Ehrenberg) Cleve, 1894	Ben	C	+	–	+	–	+	–	+	+
<i>Ulnaria ulna</i> (Nitzsch) P. Compère, 2001	Ben	C	–	–	–	–	–	–	+	–
Cryptophyta										
<i>Plagioselmis</i> sp.	–	–	–	–	–	–	–	+	–	+
Dinophyta										
<i>Alexandrium</i> sp.	–	–	–	–	–	+	–	–	–	–
<i>Amphidinium spheonoides</i> Wulff, 1919	O	AB	–	–	–	+	–	–	–	+
<i>Dinophysis acuminata</i> Claparède et Lachmann, 1859	N	C	+	–	+	–	–	–	–	–
<i>Gyrodinium fusiforme</i> Kofoed et Swezy, 1921	N	TAB	–	–	+	+	–	–	–	+
<i>Gyrodinium lacryma</i> (Meunier) Kofoed et Swezy, 1921	O	AB	–	–	–	–	–	–	–	+
<i>Oblea rotunda</i> (Lebour) Balech ex Sournia, 1973	O	–	+	–	+	–	–	–	–	–
<i>Protoceratium reticulatum</i> (Claparède et Lachmann) Bütschli, 1885	N	C	+	–	–	–	–	–	–	–
<i>Protoperidinium brevipes</i> (Paulsen, 1908) Balech, 1974	N	C	+	–	–	+	–	–	+	–
<i>Protoperidinium depressum</i> (Bailey, 1854) Balech, 1974	O	C	+	–	+	–	–	–	–	–
<i>Protoperidinium granii</i> (Ostenfeld) Balech, 1974	N	–	–	–	–	–	–	–	+	+

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Taxon	Ecological characteristic	Phytogeographical characteristic	2020				2021			
			Voevoda Bay		Novik Bay		Voevoda Bay		Novik Bay	
			I	UIW	I	UIW	I	UIW	I	UIW
<i>Protoperidinium pellucidum</i> Bergh, 1881	N	C	+	+	+	+	+	–	–	–
<i>Protoperidinium pentagonum</i> (Gran) Balech, 1974	N	Bip	+	–	+	–	–	–	–	–
<i>Protoperidinium</i> sp.	–	–	+	–	–	–	+	+	–	–
Chlorophyta										
<i>Carteria</i> sp.	–	–	–	–	–	–	+	–	+	–
<i>Chlamydomonas</i> sp.	–	–	–	–	–	–	+	–	+	–
Euglenophyta										
<i>Eutreptiella braarudii</i> Throndsen, 1969	–	–	–	–	+	+	+	+	+	+
Haptophyta										
Unidentified species	–	–	–	–	–	–	+	–	+	–

Note: N, neritic; O, oceanic; P, panthalassic; Ben, benthic; BP, bentic-planktonic; FW, freshwater; B, boreal; C, cosmopolite; AB, arctic-boreal; TB, tropical-boreal; TAB, tropical-arctic-boreal; Bip, bipolar.

In the Voevoda Bay in 2020, the highest species number was revealed for ice layers of 0–10 and 10–20 cm (22 species each), and in 2021, for the layer of 10–20 cm (28 species) (Fig. 2). Conversely, in the Novik Bay in both years, the highest species richness was found in under-ice water (19 and 22 species). Diatoms dominated the microalgal community in both biotopes accounting for 100% in one of ice layers. Pennate diatoms were significantly more diverse (53 species) than centric ones (14 species), with mean pennate-to-centric ratios of 3 : 1 and 6 : 1 in ice and under-ice water, respectively. In 2020, the diversity of centric diatoms peaked in ice layers of 0–10 and 10–20 cm in both bays (5 and 4 species); in 2021, in the lower ice layer of the Voevoda Bay, 50–62 cm (6 species), and in the mid-ice layer of the Novik Bay, 30–40 cm (4 species).

The sea-ice algal community was dominated by neritic planktonic species, primarily arctic-boreal ones (Fig. 3). The prevailing taxa varied by location, year, biotope, and sampling depth. Thus, in 2020, sea ice in the Voevoda Bay was co-dominated by *Nitzschia frigida* (up to 94% of total abundance in an ice layer) and *Thalassiosira nordenskioeldii* (up to 41%). In under-ice water, the prevailing taxa were *Nitzschia* sp. 2 (up to 41%) and *Cylindrotheca closterium* (up to 31%). In the Novik Bay, the ice community was dominated by *C. closterium* (up to 63%), *T. nordenskioeldii* (up to 55%), and *N. frigida* (up to 28%), while under-ice water was dominated by *Thalassiosira gravida* (up to 88%). In 2021, in the Voevoda Bay ice, the prevailing taxa were *Navicula septentrionalis* (up to 59%), *Nitzschia* sp. 4 (up to 46%), *Navicula granii* (up to 41%), and *Chaetoceros socialis* f. *radians* (up to 76%). Under-ice water was dominated by *Plagioselmis* sp. (up to 67%). In the Novik Bay, the ice community was characterized by the high abundance of *Nitzschia* sp. 4 (up to 72%), *N. frigida* (up to 40%), and *C. socialis* f. *radians* (up to 27%), and under-ice water community, by the high abundance of *T. nordenskioeldii* (up to 34%) and *Plagioselmis* sp. (up to 25%).

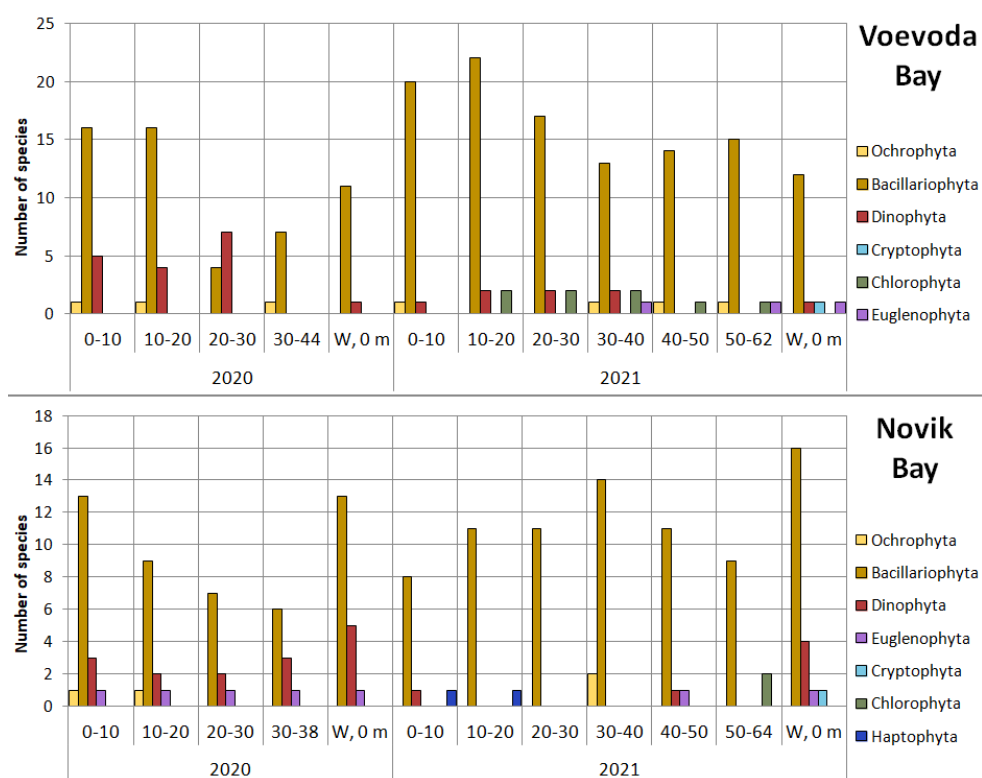


Fig. 2. Species number in samples of ice and under-ice water in the Voevoda and Novik bays

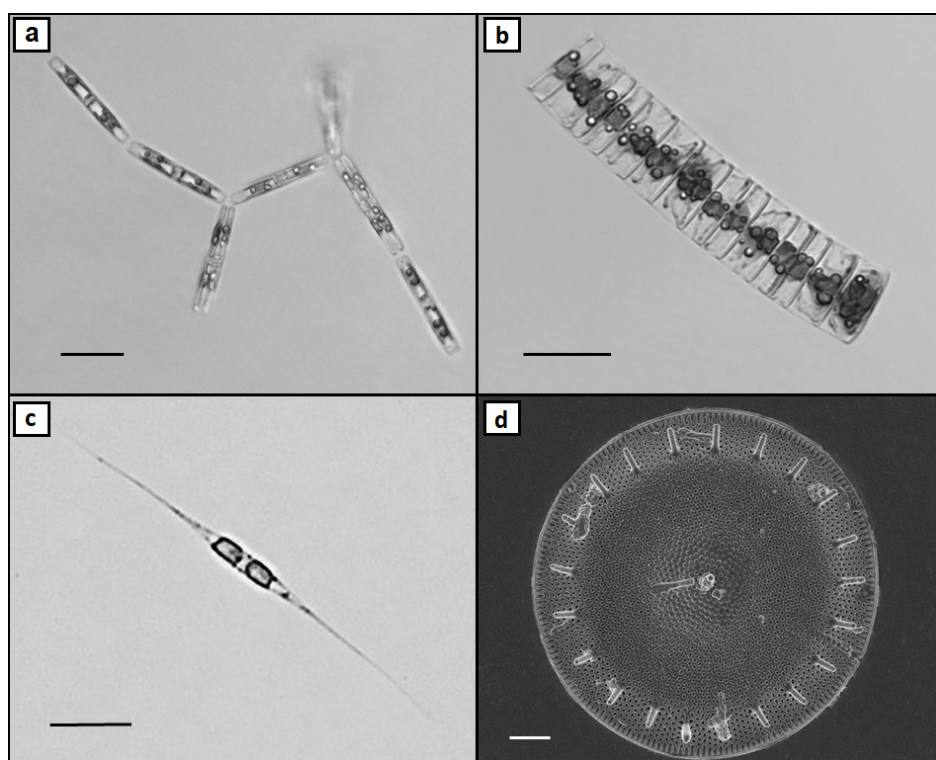


Fig. 3. Dominant microalgal species: a, *Nitzschia frigida*; b, *Navicula septentrionalis*; c, *Cylindrotheca closterium* (a light microscope); d, *Thalassiosira nordenskiöldii* (a scanning electron microscope). Scale bars are 20 μm (a–c) and 4 μm (d)

Statistical analysis revealed that microalgal community structure varied noticeably across ice layers and under-ice water, with the key drivers being biotope, sampling depth, location, and year (Fig. 4). Inter-annual variation was the most significant factor, with similarity between samples from the same year of 25% only. In 2021, communities showed pronounced spatial segregation clustering by bay, with within-bay similarity of 40%. In contrast, in 2020, there was no clear spatial pattern. The highest similarity, 65%, was recorded between several neighboring ice layers: in 2020, between those of 20–40 cm in the Novik Bay, and in 2021, between those of 30–50 cm in the Voevoda Bay and 0–20 cm in the Novik Bay.

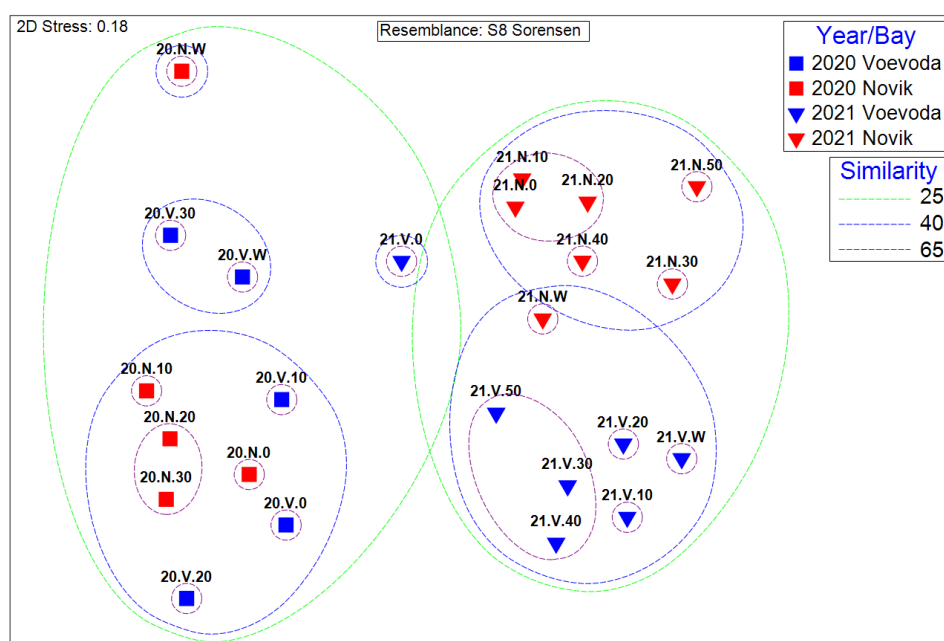


Fig. 4. Non-metric multidimensional scaling of algal flora ordination for samples of ice and under-ice water. Samples are signed according to a “year.bay.layer” pattern; a digit in a layer index indicates its upper boundary; W denotes a sample of under-ice water

DISCUSSION

The sea-ice algal communities in the Voevoda and Novik bays exhibited similar taxonomic structure, with diatoms dominating both species composition and richness [Yurikova, Begun, 2022]. Within 2020–2021, 45 species were common for two bays (52% of their total number). The similarity in algal flora in the bays can be traced through the revealed most species-rich genera. Moreover, in the Novik Bay, a higher number of represented groups were identified in each year of the study. While species richness of sea-ice microalgae was similar between two bays in 2020, the Voevoda Bay showed 1.3-fold higher richness in 2021 than the Novik Bay. The similarity in species composition likely reflects the close geographical proximity of these bays, as well as their connection with the semi-enclosed Amur Bay which features restricted water circulation. Differences in taxonomic structure are mediated by location of the bays. The Novik Bay deeply embays Russky Island, and its mouth is substantially isolated from the Eastern Bosphorus Strait; this results in the highly isolated nature of its biotope. The more exposed Voevoda Bay experiences freshwater inflow from the Russkaya River that mediates the formation of distinct microalgal community as compared to that in the Novik Bay.

Statistical analysis revealed the most significant variability in the species composition of sea ice and under-ice water samples between years of the study. In 2021, the microalgal composition in the bays was richer than in 2020, and this aligns with the data on their quantitative development [Yurikova, Begun, 2022]. This phenomenon may be attributed to specific meteorological conditions that favored the formation of a thicker ice cover than in the previous year. Differences in species composition were also affected by location (sampling site), biotope, and depth of the ice layer.

The majority of diatoms registered in sea ice of the Voevoda and Novik bays are well-documented constituents of the under-ice phytoplankton in Peter the Great Bay; it develops at sub-zero water temperatures and can attain bloom concentrations in winter and early spring [Begun et al., 2003, 2011; Kononova et al., 1989; Orlova et al., 2009; Ponomareva, 2017; Ryabushko et al., 2019; Shevchenko et al., 2020; Stonik, 2018]. A study of microphytobenthos on rocky substrates within the ice sheet of Vostok Bay in January 1980 recorded a peak diatom biomass ($2,576 \text{ mg} \cdot \text{m}^{-2}$) at a water temperature of -1.2°C , and the dominant species was a benthic-planktonic one: *Odontella aurita* (Lyngbye) C. Agardh, 1832 [Ryabushko, 1986; Ryabushko, Begun, 2015]. Interestingly, this species also occurred in the Voevoda and Novik bays. Furthermore, several species we registered have been previously reported in studies of sea-ice biota across polar regions [Buinitskii, 1973; Kauko et al., 2009; Mel'nikov, 1989; Usachev, 1949].

The common taxa in the ice algal flora of the bays of Russky Island are neritic planktonic species. However, a significant proportion of other species covered benthic (49%) and benthic-planktonic (10%) forms. Those are typical for sediment habitats or for fouling of various underwater substrates, and this can be governed by the shallow nature of the bays and the proximity of the benthic biotope. Due to wave action and uplift to the water surface, benthic species can colonize the underside of an ice cover using it as a substrate and serving as cryoperiphyton [Buinitskii, 1973; Ewert, Deming, 2013; Mel'nikov, Bondarchuk, 1987]. As known [Kauko et al., 2009], due to turbulent mixing of pelagic waters, microalgae cells are incorporated into sea ice during its formation. However, according to some researchers [Olsen et al., 2017; Ratkova, Wassmann, 2005], microphytobenthos is another source for the replenishment of the ice biotope with algal flora.

The microalgal community of Russky Island bays is a mixed planktonic diatom assemblage comprising both centric forms (predominantly pelagic) and pennate ones (usually benthic-affiliated). This reflects patterns observed in under-ice phytoplankton communities of Peter the Great Bay [Begun et al., 2011; Ponomareva, 2017; Shevchenko et al., 2020; Sorokin, Kononova, 1973]. Pennate species outnumbered centric ones by 4 times, and such a greater diversity aligns with documented successional patterns during ice algae bloom [Leu et al., 2015; Van Leeuwe et al., 2018].

Our study of sea ice in the bays of Russky Island revealed that the ice algal flora consists of both planktonic and benthic microalgae. Such a composition is mediated by the fact as follows. During the characteristic winter bloom of under-ice phytoplankton, abundant species become incorporated into the ice community with varying degrees of intensity during sea-ice formation. The intensity is associated with several complex meteorological and hydrochemical processes occurring in the water area during this period. This is reflected in the distinct species composition and quantitative abundance of microalgae [Yurikova, Begun, 2022] within each specific layer of an ice cover.

Conclusions. This survey substantially expanded data on microalgal flora of sea ice and under-ice water in Peter the Great Bay. The first comprehensive species list of cryophilic microalgae is provided. It comprises 87 taxa from 48 genera and 7 divisions. The algal flora was dominated by ben-

thic cosmopolitan species. The more exposed Voevoda Bay exhibited higher species richness but lower divisional diversity than the enclosed Novik Bay.

In 2020, 52 species from 31 genera and 4 divisions were recorded in both bays. Out of these, 36 species were noted in the Voevoda Bay, and 37, in the Novik Bay; 21 species were common for two bays. In 2021, 63 species from 41 genera and 7 divisions were registered. Out of these, 50 species were found in the Voevoda Bay, and 43, in the Novik Bay; 31 species were common. Community composition showed pronounced vertical stratification. The species composition in ice and under-ice water samples was found to vary most significantly in different years of the study.

This research was supported by the Federal Service for Hydrometeorology and Environmental Monitoring of the Russian Federation (agreement No. 169-15-2023-002).

Acknowledgements. The authors thank P. Tishchenko, P. Semkin, Yu. Barabanshchikov, and S. Sagalaev (V. I. Il'ichev Pacific Oceanological Institute FEB RAS) for field assistance. The authors are grateful to A. Lazaryuk for scientific consultation. This work was carried out at the core facility "Marine Biobank" (NSCMB FEB RAS).

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**ВИДОВОЙ СОСТАВ СООБЩЕСТВА МИКРОВОДОРОСЛЕЙ
МОРСКОГО ЛЬДА И ПОДЛЁДНОЙ ВОДЫ
В БУХТАХ ОСТРОВА РУССКИЙ
(ЗАЛИВ ПЕТРА ВЕЛИКОГО, ЯПОНСКОЕ МОРЕ)**

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Морской лёд способен выступать в качестве местообитания для микроводорослей, которые могут приспосабливаться к его уникальным условиям и успешно размножаться в нём. В настоящей работе продолжен анализ материала, впервые полученного при исследовании морского льда двух бухт острова Русский (Японское море) в 2020–2021 гг., с целью изучить послойное распределение качественного и количественного состава микроводорослей, населяющих его. В результате таксономического анализа идентифицировано 87 видов из 48 родов и 7 отделов микроводорослей. Максимальное видовое богатство представлено видами отдела Bacillariophyta (57–100 % числа видов в слое льда). Альгофлора морского льда и подлёдной воды была сформирована в основном бентосными видами, относящимися к группе космополитов. Состав доминирующих видов изменялся в зависимости от года, бухты и глубины изучаемого слоя льда; в число преобладающих видов входили *Chaetoceros socialis* f. *radians*, *Cylindrotheca closterium*, *Navicula septentrionalis*, *Nitzschia frigida*, *Thalassiosira gravida*, *T. nordenskiöldii* и *Plagioselmis* sp. Наиболее значительно видовой состав различался между годами исследования, а также в зависимости от бухты, биотопа и расположения слоя в толще льда.

Ключевые слова: ледовая альгофлора, диатомовые водоросли, Японское море