

Article

Phytoplankton of the High-Latitude Arctic: Intensive Growth Large Diatoms *Porosira glacialis* in the Nansen Basin

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Abstract: In August 2020, during a dramatical summer retreat of sea ice in the Nansen Basin, a study of phytoplankton was conducted on the transect from two northern stations in the marginal ice zone (MIZ) (north of 83° N m and east of 38° E) through the open water to the southern station located in the Franz Victoria Trench. The presence of melted polar surface waters (mPSW), polar surface waters (PSW), and Atlantic waters (AW) were characteristic of the MIZ. There are only two water masses in open water, namely PSW and AW, at the southernmost station; the contribution of AW was minimal. In the MIZ, first-year and multiyear ice species and Atlantic species were noted; Atlantic species and first-year ice species were in open water, and only ice flora was at the southernmost station. The maximum phytoplankton biomass ($30 \text{ g} \cdot \text{m}^{-3}$) was recorded at the northernmost station of the MIZ, and 99% of the phytoplankton consisted of a large diatom *Porosira glacialis*. Intensive growth of this species occurred on the subsurface halocline separating mPSW from PSW. A thermocline was formed in open water south of the MIZ towards the Franz Victoria Trench. A strong stratification decreases vertical nutrient fluxes, so phytoplankton biomass decreases significantly. Phytoplankton formed the maximum biomass in the thermocline. When moving south, biomass decreased and its minimum values were observed at the southernmost station where the influence of AW is minimal or completely absent. A transition from the silicon-limited state of phytoplankton (MIZ area) to nitrogen-limited (open water) was noted.

Keywords: phytoplankton; large diatoms; marginal ice zone; nutrients; high-latitude Arctic; Nansen Basin



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1. Introduction

Global warming is most clearly manifested in the Arctic and is associated with a dramatic decline in sea ice extent and thickness [1–4]. In the Eurasian Basin, these phenomena are not associated with atmospheric processes but primarily with the increased influence of warm and salty waters of Atlantic origin (Atlantic Water, AW) [5–7]. Seasonal variability of the temperature of AW at the border of the Arctic Basin plays an important role [8].

The reduced role of water masses of the Arctic origin (ArW) and an increased role of AW have changed the vertical hydrophysical structure in the Arctic Ocean and the Barents Sea [5,9–11]. In the last 15–20 years in the eastern Arctic Ocean, the increased oceanic heat flux from an intermediate depth of approximately 150–900 m shifted warm AW to the mixed surface layer, which led to a decrease in the ice cover [10]. The implications of such changes include ecosystem restructuring and replacing native species with North Atlantic species [12–14]. The totality of these processes is commonly known as “atlantification” [6,8,15,16]. Highly saline and nutrient-rich (nitrogen, phosphorus, and silicon) AW due to thermal convection can enter the euphotic zone under certain conditions [17,18], which hypothetically should stimulate the primary production (PP). The effect of climate change in the Arctic may affect the micronutrient availability (iron, manganese, copper, zinc, cobalt, and nickel) from Siberian rivers that may potentially impact

the phytoplankton and PP in the Arctic open water and the high-latitude North Atlantic Ocean [19].

Previously, it was assumed that the Arctic Ocean ecosystem had low productivity caused by the light limitation of phytoplankton growth due to its absorption by multiyear ice. However, there is currently a change in this paradigm [20–23]. It was shown that high phytoplankton biomass forms on the lower border of the ice in the summer, and this zone becomes highly productive. Consequently, the role of the Arctic Ocean in the functioning of the climate-forming biological carbon pump increases. Ice cover is a habitat of phytoplankton, and the PP of the ice flora may be comparable to that of pelagic algae [24]. The multiyear ice is replaced by the first-year ice [25]; these types of ice have different physical structures and, as a result, different phytoplankton species compositions [26–28]. The supposition is that ice-free water would grow its PP [29], but the available estimates of an increase in PP differ [23,30,31]. The phenomena associated with “atlantification” were most studied in the Barents Sea [32,33], where significant shifts in the manifestation of seasonal dynamics and phenology of phytoplankton blooms were noted [34,35]. In the summer, the intensity of coccolithophore *Emiliania huxleyi* blooms increased, and the fields of this species’ distribution were expanding. [16,36].

To the north, detailed investigations were conducted around the Svalbard archipelago and on the shelf around the island of Kvitøya, in the trench of the same name and in the western part of the Nansen Basin above depths not exceeding 1000 m [37–40]. In August 2017, the structure of phytoplankton in the Franz Victoria Trench and the adjacent shelf of the northern Barents Sea were studied [40]. Only a few studies are known concerning the ice flora in the deep high-latitude Arctic Basin [26,28,37] and open-water species after phytoplankton blooms [41].

To the north of Svalbard in the Nansen Basin, the last decade saw a noticeable retreat of the ice cover and the appearance of large areas of open water due to thermal convection [42,43]. In this area, warm AW meets cold polar waters and creates a complex hydrographic vertical structure [44] with low predictability of consequences for the ecosystem. Direct (on-board) measurements of marine phytoplankton in the deep Arctic high-latitude open water basin have not been carried out to date. As a result, the question of phytoplankton’s structural and functional organization during the transition period from an ice-covered area of open water remains to be determined. The increase in PP in MIZ has been known for a long time [45], but its mechanisms remain unexplored. Knowledge about shifts in the species composition of phytoplankton and its productivity during the retreat of the ice edge to the north is necessary for predicting the response of high-latitude ecosystems to climate change.

In the summer of 2020, a dramatic shift of the ice edge far to the north and east was observed in the Nansen Basin, which made it possible to conduct ship observations in the open water. Our research was carried out on the transect from the northern stations of the MIZ zone above a depth of 3000 m to the southern shelf stations in the Franz Victoria Trench. We set the following goals for our research:

1. To obtain data on water masses and hydrophysical, hydrochemical, and optical properties of water;
2. To investigate the phytoplankton composition in the MIZ area and open water at stations with different ratios of polar and Atlantic waters;
3. To understand the mechanisms of increasing productivity in MIZ and to test the hypothesis about halocline’s determining role in forming a highly productive zone;
4. Flora composition is a biomarker of the ice age, so knowing the phytoplankton allows us to test the following hypothesis: In the Nansen Basin, there was a significant shift in the ice cover formation, namely, the replacement of the multiyear ice with the first-year ice.

2. Methods

2.1. Field Studies

The field data were obtained in the Nansen Basin and the northern part of the Barents Sea during the cruise 80 of the RV *Akademik Mstislav Keldysh* on 16–19 August 2020 (Figure 1, Table S1). Stations A and B are located above a depth of over 3000 m at MIZ, station C is above the deep water, stations D and E are above the continental slope, and stations F and Gare are at the outlet of the deep water of the Franz Victoria Trench to the west of the Franz Josef Land archipelago. Vertical temperature and conductivity profiles were carried out at each station from the water surface to the seafloor. An SBE9p system equipped with 10-L Niskin bottles was used, along with an SBE 9+ CTD with a temperature sensor (measurement accuracy up to 0.001 °C) and a salinity sensor (accuracy up to 0.001) and a pressure sensor (0.001 hPa). Sampling was carried out from different depths selected by CTD probing (Table S2–S4). Hydrophysical parameters were measured twice at station A on August 17 at 7:29 and 13:23 UTC. At station B (6861) on August 18, the beginning of measurements corresponded to 3:05 and 7:06 UTC.

2.2. Species Identification

Species identification was based on morphology and was conducted following [46,47] and the World Register of Marine Species (<http://www.marinespecies.org>). The cells were identified and counted using an Ergoval light microscope (Karl Zeiss, Jena, Germany) with 16 × 10 and 16 × 40 magnifications.

Cells with linear dimensions below 20 µm were counted using a Naujotte chamber (0.05 mL); the large cells were counted using a Naumann chamber (1 mL). Unidentified species of the size group 4–10 µm were assigned to the small flagellate group. Cells with linear dimensions less than two µm were not considered when estimating total phytoplankton biomass. Cell biovolume and biomass were estimated, according to [48]. Wet phytoplanktonic biomass has been converted to carbon using allometric equations [49]. The dominant species were those with biomass that exceeded half the total phytoplankton biomass.

2.3. Nutrient Analyses and Chlorophyll a and Primary Production Determinations

Analyses of phosphate phosphorous ($P - PO_4^{3-}$), dissolved silicate (Si), nitrate ($N - NO_3^-$), nitrite ($N - NO_2^-$), and ammonia ($N - NH_4^+$) nitrogen were carried out with a segmented continuous-flow TechNicon II autoanalyzer or with colorimetric methods [50,51].

Chlorophyll a and pheophytin concentrations were assessed fluorometrically according to Holm-Hansen and Riemann [52]. Whatman GF/F glass fiber filters with trapped material were extracted in 90% acetone (at 2 °C in the dark for 24 h). The fluorescence of the extracts was measured with a Trilogy laboratory fluorometer version 1.1 (Turner Designs, San Jose, CA, USA) before and after acidification with 1 N HCl. The accuracy of determination was $\pm 0.02 \text{ mg} \cdot \text{m}^{-3}$.

PP measurements were conducted using the ^{14}C -bicarbonate incorporation method [53], where 100 µL of ^{14}C -bicarbonate (5 µCi/mL) was added per 310-mL. Samplers were collected on the base of CTD profiles at 7 depths corresponding to levels of photosynthetically available radiation (PAR) in the range from 90 to 0.1% of surface flux. Duplicate subsamples of each depth and one sample subjected to dark conditions (covered with aluminum foil) were incubated for periods of 24 h in neutral density screens in an on-deck-type incubator. The seawater was continuously pumped through the incubator to maintain the temperature at an *in situ* value using an aquarium chiller (TECO TK, Italy). The samples from station A were incubated in the sea suspended at depths of 0.5, 5, 10, 15, 20, 25, 30, 35, 40, and 74 m. After incubation, the samples were filtered through nylon filters (Technofilter RME, Vladimir, Russia) with a pore size of 0.2 µm, further cleansed with 1% *v/v* hydrochloric acid, and then fixed with 10 mL scintillation cocktail (EcoLume, MP Biomedicals, Rockville, MD, USA). The incorporated ^{14}C was determined by a scintillation counter (TRI-Carb TR, Packard, Detroit, MI, USA).

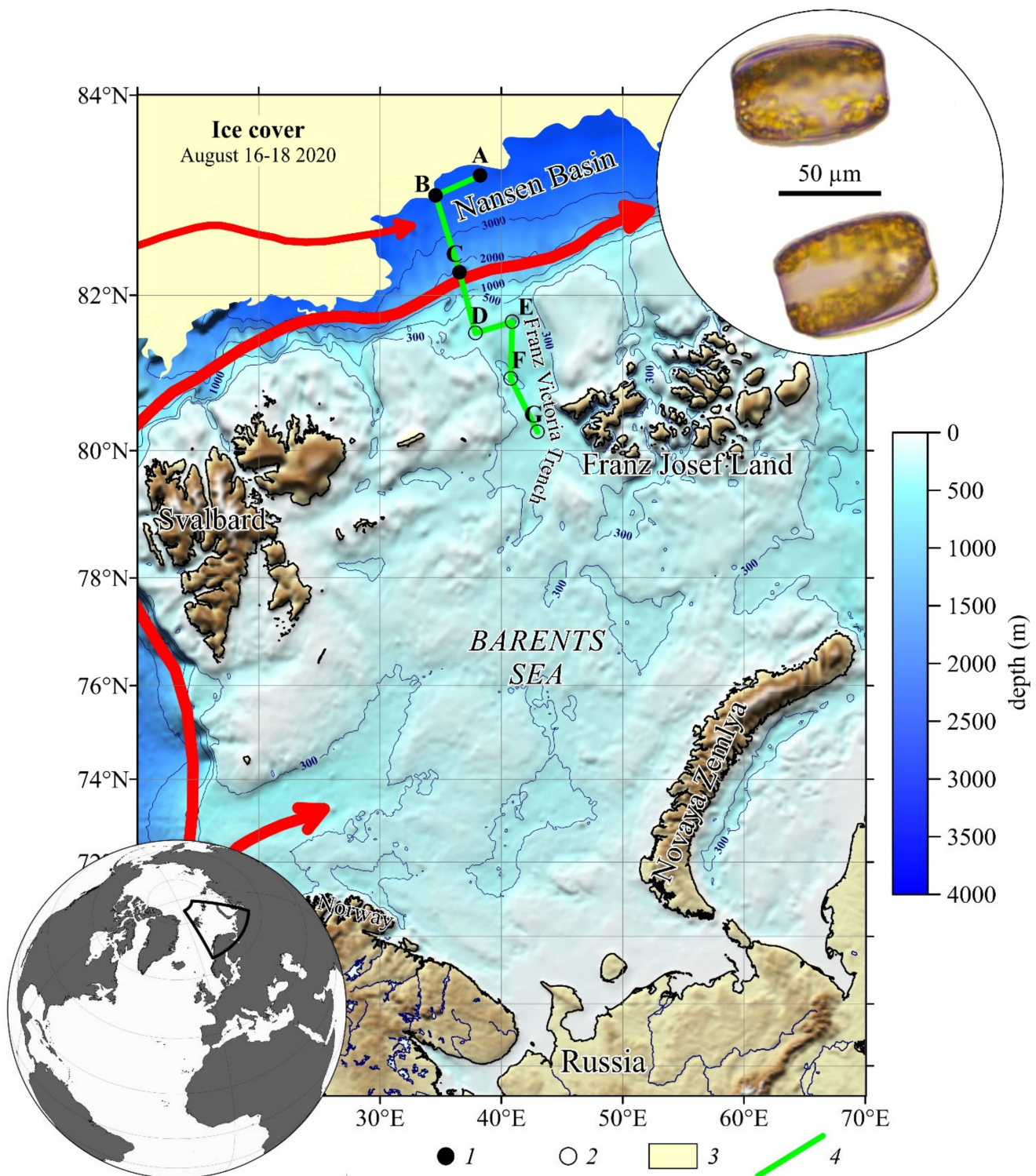


Figure 1. The map of sampling stations in the Nansen Basin and the Barents Sea in August 2020: (1) deep water stations; (2) shelf stations; (3) ice edge position; (4) transect position. Based on GEBCO bathymetry. Image of the ice cover is composited over 16–18 August 2020, provided by State Research Center “Arctic and Antarctic Research Institute”: electronic atlas http://www.aari.ru/odata/_d0015.ph (accessed on 25 September 2020).

2.4. Optical Measurements

Measurement of PAR (400–700 nm) was performed using devices manufactured by LICOR Environmental, Lincoln, NE, USA. The LI-192 sensor was used to measure underwater

irradiance. The irradiation measurements on the sea surface were carried out using the LI-190SA sensor, which was located on the deck to minimize the effect of shadows from the superstructure of the ship.

The diffuse PAR attenuation coefficient K_d was calculated using the exponential law of variation of incident downwelling irradiance $E_d(z)$ with depth z [54]:

$$E_d(z) = E_d(0) \cdot e^{-K_d z}$$

The euphotic depth (z_{eu}) was calculated as the depth where $E_d(z)$ was reduced to 1% and 0.1% of surface irradiance:

$$z_{eu} = -\ln\left(\frac{a}{K_d}\right)$$

$$a \equiv \frac{E_d(z)}{E_d(0)} = 0.01 \text{ or } 0.001$$

3. Results

3.1. Hydrophysical Conditions

In the abnormally warm summer period for the Arctic in 2020, in the deep water of the Nansen Basin, the boundary of the ice fields was fixed at approximately 83° N. (Figure 1). The water surface temperature ranged from −1.43 to −1.49 °C at stations A and B (Figure 2; Table S2). Surface water at C–G stations had temperatures > 0 °C. At all stations, the presence of a desalinated layer with salinity from 30.72 to 33.69 was recorded on the surface. In contrast, the salinity increased in the southward direction from station A to station G. Water density showed a similar spatial distribution pattern. The upper desalinated melting water was separated by halocline from the underlying waters at stations A and B. The depth of the halocline at station A did not change between the two measurements during the day; at station B, there was a shift of the halocline to the water surface by more than 5 m after 4 h (Table S1). The presence of a seasonal thermocline characterized the other stations, the depth of which increased significantly southward from station C to station G and there was a significant shift in the pycnocline and halocline. Colder waters with a relatively low core temperature (up to −1.77 °C) and low salinity (from 34.15 to 34.56) were located below the halocline. Spatial heterogeneity of the temperature distribution in the core was observed with a tendency to increase from station A to station G. In contrast, the temperature at stations A, B, and C is significantly lower than the temperature of the other stations (*t*-test, $p < 0.05$). The core depth of the lowest temperatures has virtually not changed at all stations except for stations B and G, where the core was much more profound.

Below these waters, the temperature, salinity, and density increased and reached their highest values (up to 2.66 °C at station B). At stations A, B, and C, the salinity in the core of the maximum temperature exceeded 34.9 (Table S2). At the other stations, this value was lower. There was no water with temperature > 0 °C at station G. A tendency for the core temperatures to decrease along the section was noted. In contrast, the temperature at stations A, B, and C significantly differed from the core temperature at stations D, E, and F (*t*-test, $p < 0.05$). The depth of the core of the maximum temperatures was deeper at stations A, B, and C; at the rest of the stations, it was 72 m closer to the surface (*t*-test, $p < 0.05$).

3.2. The Distribution of Water Masses

The names of the water masses mainly correspond to the definitions given by Perez-Hernandes et al. [55]. Surface waters at stations A and B represented melted polar surface waters (mPSW), characterized by the lowest salinity and density (Figures 2 and 3; Tables 1 and S2). The temperature varies within very narrow boundaries. Below this layer lie polar surface waters (PSW), which have a low temperature in the core whose position did not fall below the depth of 75 m (Figure 2, Table 1). Relatively low salinity and low density were characteristic of this water mass. The core's depth of warm AW located below the PSW was not deeper than 250 m. This water mass was characterized by high salinity and density. There was no AW at station G. Below the core of the AW, the temperature began to

decrease to negative values. This water mass is characterized by the Arctic intermediate waters (AIW), which extend through the water column to the bottom of the Nansen Basin.

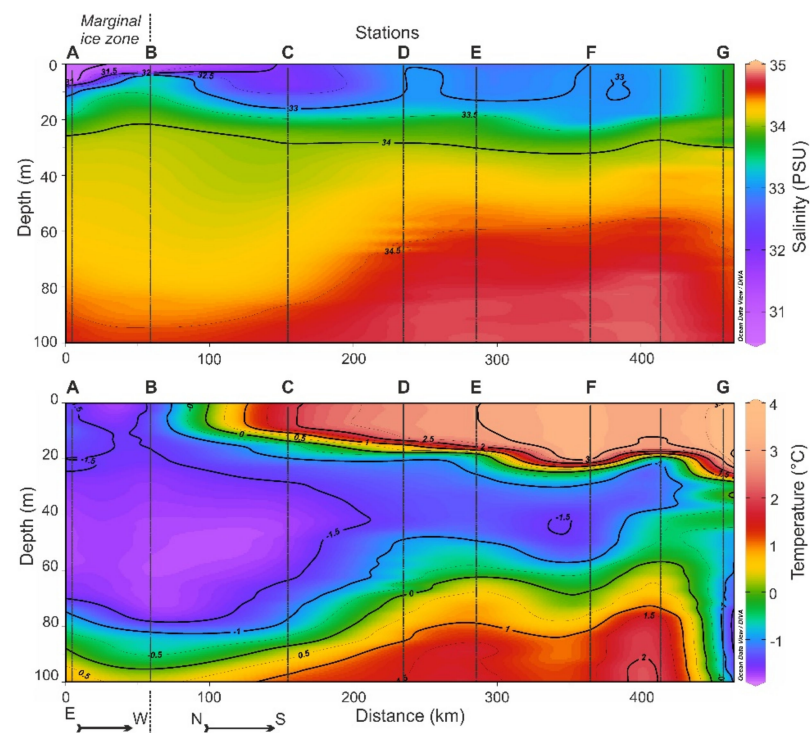


Figure 2. Temperature and salinity profiles along the cruise track (stations A–G) shown in Figure 1.

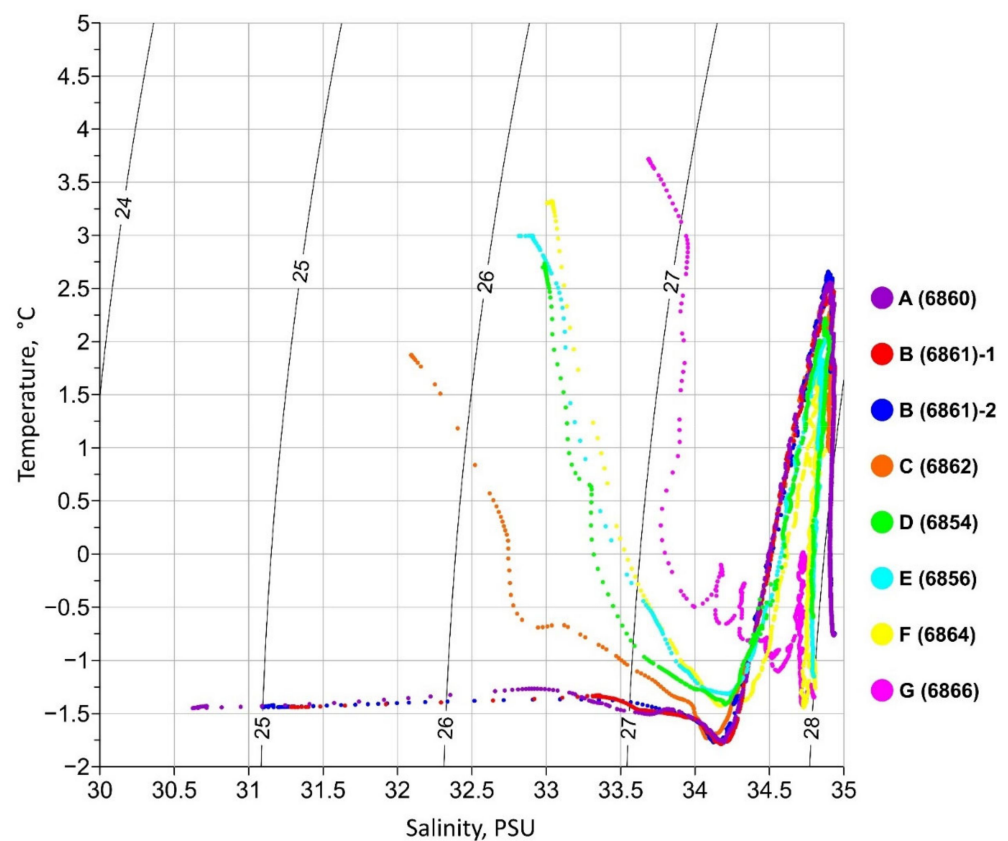


Figure 3. Temperature–salinity plots of all stations in August 2020.

Table 1. Changes in temperature, salinity, and density in the core of AW and PW, as well as the minimum temperature in mPSW and maximum temperature in PSWw at the stations of the studied area.

Water Mass	Potential Temperature (ϑ), °C	Salinity (S), PSU	Density (σ), kg m ⁻³
AW	1.77 < ϑ < 2.66	34.84 < S < 34.92	27.83 < σ < 27.87
PSW	−1.77 < ϑ < −1.1	31.09 < S < 34.56	25.0 < σ < 27.8
mPSW	−1.49 < ϑ < −1.427	30.72 < S < 31.28	24.69 < σ < 25.15
PSWw	1.87 < ϑ < 3.72	32.09 < S < 33.69	25.6 < σ < 26.77

3.3. Hydrochemical Conditions

Very low concentrations of macronutrients were observed at station A in the surface water up to a layer of 11 m (Table S3), and concentrations capable of supporting phytoplankton growth were recorded only from a depth of 22 m. At station B, relatively high concentrations of P – PO₄^{3−}, N – NO₃[−], and Si were observed in the layer of 9 m. At station C, only at a depth of 31 m, the concentration of N – NO₃[−] exceeded 1 µM, and the concentration of Si remained relatively low. At station D, the concentration of N – NO₃[−] was very low up to a depth of 28 m with relatively high concentrations of Si and P – PO₄^{3−}. At station E, N – NO₃[−] was not detected up to a depth of 16 m, and at stations F and G up to a depth of 21 m. Finally, at station H, at a depth of 28 m, very low concentrations of N – NO₃[−], and Si were found, which are not capable of providing photosynthetic processes.

When comparing different water masses, it should be noted that mPSW and PSW are characterized by low Si concentrations. In PSW and AW, the concentrations of all nutrients are higher, while in AW, they are significantly higher than in PSW (*t*-test, *p* < 0.05) (Table 2). AW's nitrogen-to-phosphorus molar ratio is much higher and close to the Redfield ratio.

Table 2. Minimum, maximum, and average concentrations of dissolved silicon, phosphorus phosphates, nitrogen nitrites, and nitrates, as well as the ratio of nitrogen and phosphorus in AW and PSW at all studied stations.

Water Mass		Temp °C	Salinity PSU	Si µM	P-PO ₄ ^{3−} µM	N-NO ₂ [−] µM	N-NO ₃ [−] µM	N _{min} Total µM	N:P
PSW	min	−1.74	34.04	0.16	0.29	0.04	1.05	1.10	3.81
	max	−1.09	34.72	3.76	0.79	0.22	9.39	9.50	14.50
	average	−1.45	34.29	1.84	0.49	0.11	5.42	5.52	10.79
AW	min	1.22	34.64	3.97	0.63	0.00	9.54	9.60	13.35
	max	2.53	34.92	5.33	0.79	0.06	12.33	12.34	17.15
	average	1.92	34.82	4.70	0.72	0.03	10.89	10.93	15.09
<i>t</i> -test	<i>p</i>			10 ^{−6}	10 ^{−3}			10 ^{−5}	10 ^{−3}

3.4. Light Conditions and Optical Characteristics of Water

The PAR on the water surface varied during the day in 20–625 µM photons·m^{−2}·s^{−1}. High and variable cloudiness significantly moderated the incident solar radiation. At the time of the sampling, the radiation on the surface varied from 59 to 279 µM photons·m^{−2}·s^{−1} (Table 3). The maximum diffuse PAR attenuation coefficient *K_d* values were at station A (depths from 0 to 20 m) (Table 4). At station B, the maximum *K_d* values were observed in a layer from 0 to 10 m; at station C, a layer from 20 to 40 m was characterized by the maximum light diffuse attenuation. At stations D and E, the maximum attenuation layer shifted towards greater depths. At stations F and G, the layer with maximal *K_d* values was the surface water.

Table 3. Irradiance ($\mu\text{M photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at the water surface and at a depth of 3 and 10 m, as well as the depth where the irradiance is 1% and 0.1% of the surface irradiance.

Station	Irradiance			Depth, m	
	Surface	3 m	10 m	1%	0.10%
A	184	124	50	35	74
B	169	115	47	46	91
C	148	109	54	30	38
D	279	201	94	39	50
E	144	110	59	43	66
F	139	101	49	60	>100
G	59	40	11	64	>100

Table 4. The diffuse PAR attenuation coefficient K_d at different depths, as well as the integral coefficient for a layer of 50 m.

Station	K_d (0–50 m)	K_d (0–10 m)	K_d (10–20 m)	K_d (20–30 m)	K_d (30–40 m)	K_d (40–50 m)
A	0.067	0.131	0.147	0.073	0.072	0.066
B	0.061	0.128	0.095	0.072	0.072	0.065
C	0.100	0.087	0.062	0.242	0.297	0.086
D	0.108	0.089	0.057	0.064	0.198	0.245
E	0.097	0.050	0.060	0.066	0.109	0.159
F	0.057	0.104	0.054	0.061	0.065	0.070
G	0.054	0.125	0.044	0.053	0.065	0.056

The minimum depth of the euphotic layer, defined as 1% of the surface radiant, is minimal at stations A and C and does not exceed the depth of 30 m. The greatest depths of the euphotic layer were at stations F and G.

3.5. Structure and Biomass of Phytoplankton

The Nansen Basin. One hundred six species of phytoplankton belonging to six systematic groups have been found in the Nansen Basin. Algae of four ecological groups played the main role in the diatom component (Table 5):

1. Species associated with the multiyear ice;
2. Species associated with the first-year ice [26];
3. Atlantic species of spring blooms in open-water areas (*Chaetoceros gelidis*, *Eucampia groenlandica*, *Phaeocystis pouchettii*, *Pseudo-nitzschia delicatissima*);
4. Large Atlantic oceanic species of the summer complex from the genus *Chaetoceros*, *Rhizosolenia* and *Sundstroemia*.

The dinoflagellates of the genus *Alexandrium*, *Gonuaulax*, *Gymnodinium*, *Gyrodinium* and *Protoperdinium* were represented by cells of various size groups belonging to both the nano- and the microphytoplankton. Among the Prymnesiophyceae species, the Atlantic species *Phaeocystis pouchettii* played the main role. Among the species of the other systematic groups, the coccolithophore *Emiliania huxleyi* and *Coccolithus pelagicus*, should be indicated. The species structure at all three stations in the Nansen Basin demonstrated a high degree of similarity in the 50–60% range according to the Sorensen criterion. The highest similarity index was registered between stations A and C.

Table 5. Vertical location (m) of species of the main phytoplankton complexes in the Nansen Basin and the northern shelf of the Barents Sea.

		Stations						
Species		A	B	C	D	E	F	G
I. The species associated with multiyear ice								
1.	<i>Chaetoceros septentrionalis</i>	0						
2.	<i>Fossila arctica</i>	0–5						
3.	<i>Fragilariopsis cylindrus</i>	0, 20	3	0, 30				
4.	<i>Melosira arctica</i>	0						
5.	<i>Nitzschia frigida</i>	0, 10, 30						
6.	<i>Pauliella taeniata</i>	0–5, 25						
7.	<i>Pennate</i>	0–5	0–24	22				
II. The species associated with second-year ice								
1.	<i>Thalassiosira bioculata</i>			2				
III. The species associated with first-year ice								
1.	<i>Porosira glacialis</i>	0–25, 200, 800, 3000	0–15	602	7, 28–38	50–140	111, 571	
2.	<i>Thalassiosira gravida</i>	0–40, 74, 3000	0–15, 34–600	2–45, 100	20–38, 100, 400	40–100,	100, 111, 571	66
3.	<i>T. nordenskioldii</i>	0, 20		2–45	27–38	50, 140		
4.	<i>T. hyalina</i>	0, 20 40		38–45, 100	200	140	111	
5.	<i>T. rotula</i>	0–35		6–45, 22–38				
6.	<i>T. antarctica</i> f. <i>borealis</i>	20						
IV. The Atlantic open water species								
1.	<i>Chaetoceros gelidis</i>	0–30	0–46, 72	2, 10, 30	38	10		
2.	<i>Eucampia groenlandica</i>	0–25		16–45	27–38			
3.	<i>Phaeocystia pouchetii</i>	200		38–45	27–38	40		
4.	<i>Chaetoceros compressus</i>	0–5	24					
5.	<i>Pseudo-nitzschia delicatissima</i>	0–25			38			
6.	<i>Rhizosolenia hebetata</i>	25–30,	34, 72, 91					
7.	<i>R. hebetata</i> f. <i>semispina</i>	5, 20–40	46, 72	0, 22, 30	7, 20, 27, 38	26–40		
8.	<i>Sundstroemia setigera</i>	25–35	34–46, 72	30–38, 45				
9.	<i>R. styliformis</i>	10, 25, 30	46	30–38	7			

Table 5. Cont.

		Stations						
Species		A	B	C	D	E	F	G
10.	<i>Chaetoceros atlanticus</i>		46, 72	38–45				
11.	<i>C. borealis</i>	30	46, 72				46	12
12.	<i>C. danicus</i>		34, 46					
13.	<i>Prorocentrum minimum</i>	20–30	0–46, 100	10	25–38	03.05.1940	4–30, 60	0, 4, 20
14.	<i>P. islandicum</i>	0, 20		0–30	0, 7, 12, 38	16–26		
15.	<i>Coccolithus pelagicus</i>		185					
16.	<i>Emiliana huxleyi</i>	35		10, 602	0		0, 4, 20	
17.	<i>Ph. pouchetii</i>	200		28–45	27–38	40		
18.	<i>Monochrysis</i> sp.			2	0–100	0–40	4–100	0–20

In MIZ, the large centric diatom *Porosira glacialis* was the dominant species. At station A, in the layer of the sharp-gradient halocline, biomass reached $30 \text{ g} \cdot \text{m}^{-3}$ ($799.07 \text{ mg} \cdot \text{C} \cdot \text{m}^{-3}$), and the community's biomass was 99% formed by this species (Tables S4 and S5). Species of the first-year and multiyear ice flora and Atlantic species were noted here (Table 5). At the border of the photic zone of the layer of 35 m, the coccolithophore *Emiliania huxleyi* was singly marked. In the AW's 100–800 m water layer, the diatom component was represented by spores of *P. glacialis*, *Thalassiosira gravida*, and *Thalassiosira* spp. Large dinoflagellates of the genus *Diplopsalis*, *Torodinium*, and *Dinophysis* were found at the main pycnocline. At the core of AW (depth of 200 m), in addition to small-cell *Gymnodinium*, cells of the *Phaeocystis pouchettii* were found singly.

At station B, as at station A, *Porosira glacialis* were the dominant species, and the maximal biomass of phytoplankton was concentrated in the upper 10 m layer above the sharp gradient halocline. The community's biomass did not exceed $22 \text{ mg} \cdot \text{m}^{-3}$ (Tables S4 and S5). Atlantic diatoms and species of ice flora were found in the euphotic zone.

Dinoflagellates were dominant at station C's surface water layer; a small biomass maximum of this group was at the lower boundary of the seasonal thermocline (Tables 5, S4 and S5). Diatoms of the genus *Thalassiosira*, *Eucampia*, *Pseudo-nitzschia*, *Rhizosolenia*, *Sundstroemia*, *Chaetoceros*, dinoflagellates *Prorocentrum minimum*, and coccolithophore *Emiliania huxleyi* are embedded within the euphotic zone. Outside the euphotic zone, in the layer of 100 m the flora of the first-year ice was represented by genus *Thalassiosira*. At the core of AW at a depth of 245 m, the diatom *Lauderia borealis* was observed at the sporulation stage. At a depth of 602 m in the AW, the coccolithophore *E. huxleyi* reached the maximum abundance for the whole study area.

The area of the continental slope (stations D, E). The maximum dinoflagellates abundance and biomass were recorded at a seasonal thermocline (Tables 5, S4 and S5). These maxima were formed by species of the genus *Gymnodinium*, *Gyrodinium*, *Alexandrium*, *Protoperidinium*, and *Prorocentrum* were also noted here. The diatoms component consisted of species of the first-year ice observed at both stations. At station D, they were accompanied by species of open water such as *Eucampia groenlandica*, and at station C, by species of the first-year ice flora *Porosira glacialis*. The Atlantic dinoflagellate *Prorocentrum minimum* and the diatoms genus *Thalassiosira* and *Porosira* were found in the core of AW.

The Frantz Victoria Trench. Compared with deep-water stations in the Nansen Basin, the phytoplankton was characterized by low species diversity, mainly due to the reduction of the diatom component (Table 5). The lowest similarity indices (25–26%) with station C were also revealed. Abundance and biomass were also low (Tables S4 and S5). At station F, the maximum phytoplankton biomass was formed by small flagellates, chrysophyte of genus *Monochrysis*, and the large dinoflagellates of the genus *Gymnodinium* and *Gyrodinium*. The phytoplankton biomass did not exceed $37 \text{ mg} \cdot \text{m}^{-3}$ and $4.6 \text{ mg} \cdot \text{m}^{-3}$ at stations F and G, respectively. At station F, at AW's core, first-year ice species were diatoms of the genus *Thalassiosira* and dinoflagellates *Gymnodinium* spp. and *Protoperidinium brevipes* were found. In the MIZ, first-year, and multiyear ice; Atlantic species were also noted. Atlantic species and first-year ice species were found in open water, and in the deep-water part of the Nansen Basin, the multiyear ice was replaced by the first-year one. Only first-year and multiyear ice floras were present at the southernmost station. Furthermore, intensive growth (up to $30.0 \text{ g} \cdot \text{m}^{-3}$) of the large centric diatom *Porosira glacialis* was found in the MIZ area. The dominance of this species and such biomass in the MIZ was discovered for the first time. This result is unexpected since it is well known that the intensive growth of diatoms with smaller cell sizes as species of multiyear ice is expected in the high latitudes of the Arctic. At Station G at a depth of 113 m, with a maximum temperature of about zero and a salinity of 34.7, only *Thalassiosira* spp. spores and small species of genus *Gymnodinium* were observed in the PSW.

4. Discussion

4.1. Environmental Conditions

The reduction of the Arctic ice cover has been a dominant trend over the past several decades [2,4,25]. However, the ice situation in the waters north of Svalbard is very dynamic. It has significant interannual variability, as shown by direct observations [41], and this study undoubtedly applies to the Nansen Basin. During our 2020 measurements, the ice edge retreated northwards and eastwards (Figure 1), and in 2021 only a very small western part was ice-free [56]. The reduction of sea ice is explained by two main hypotheses that link this process either with an increase in atmospheric temperature or an increase in the influence of AW [6,23,57,58]. Our data show that the depth of the water layer with a temperature of 1 °C in the MIZ area (stations A and B) is about 100 m. In contrast, at open-water stations, the heat transfer at the atmosphere-seawater interface is decisive, contributing to the formation of a seasonal thermocline, which follows from the analysis of the T, S diagram (Figure 3).

To describe the hydrography of the Nansen Basin based on the existing definitions of water masses close to our research area [18,59,60], we chose the names of water masses given in the work of Perez Hernandez et al. [55] with some changes. The Nansen Basin receives warm AW from both the Svalbard branch of the West Svalbard Current (SvB) and the more northern branch passing through the Yermak Plateau—Yermak branch (YB) of the AW [5,59]. When moving to the east, these waters transform due to changes in thermohaline properties.

In September 2012, above the continental slope to the north of the Kvitøya Trough (81.5° N, 31° E), the AW core was usually located at a depth of 100 to 500 m, where temperature and salinity exceeded 3 °C and 35, respectively [44], and the water temperature was even higher in the west [19]. In September 2013, studies in the area of 80° N–83° N and 18° E–34° E by Perez-Hernandes et al. [55] distinguished AW with the following characteristics: $\sigma > 27.6$, $S > 34.9$ and $\vartheta > 1$. In 2020, AW displayed these properties only at stations A and B (Figure 1, Table 1). The core of the AW was above 200 m, indicating the AW's rise. Compared with the SvB, the temperature and salinity in the core have significantly decreased, which indicated a pronounced transformation of this water mass.

The relative contribution of different water masses varies greatly when moving along the section southward. For example, if PSW is present at all stations, mPSW is typical for stations A and B, AW is registered from station A to station F, and PSWw is located south of station C. At the same time, there is a transformation of water masses along the section, when moving south, AW becomes colder, and PSW becomes warmer.

Due to the exchange with cold polar waters, heat losses in the Nansen Basin are relatively high [61]. This phenomenon provides a relatively high vertical turbulent flux of nutrients to the upper water layers and the transfer of Atlantic flora from the AW to the photic zone. The temperature and salinity in the core have significantly decreased, which indicates a pronounced transformation of this water mass.

4.2. Light Conditions and Optical Characteristics of Water

The rate of organic matter production due to photosynthesis is determined by the flux of light energy absorbed by phytoplankton pigments. In turn, the chlorophyll content in the cell is a function of the irradiance; with increasing light intensity, this parameter decreases [61–64]. The rate of photosynthesis as a function of light intensity is a hyperbolic curve [65]. At high light fluxes, the rate of photosynthesis can be inhibited. This process depends on the adaptation strategy, which is different in different species, determined by the size and shape of cells and the nutrient concentrations [62–68]. The fundamental characteristic is the light intensity at which photosynthesis saturation occurs, which is an inverse function of temperature [69]. The maximum rate of photosynthesis of natural phytoplankton and the intensity of light-saturating photosynthesis depends on latitude [70]. For high latitudes, the optimal light intensity is about 60 $\mu\text{M photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [71]. Light intensities close to this value were recorded at the stations of the Nansen Basin at a depth

of 10 m (Table 5). Moving the halocline to a depth of 3 m leads to doubling the light flux intensity and brings the cells into the photoinhibition zone. In addition, the adaptation of cells is important; with prolonged maintenance in low light, the saturating light intensity decreases [72]. Thus, the vertical movement of halocline in the water column is of fundamental importance: the structure of phytoplankton changes towards the dominance of those species that have a higher tolerance to the variation of the light intensity. Our PAR data obtained during this study illustrate the dynamic nature of light in the high Arctic (Figure S1). The irradiance on the sea surface changes by order of magnitude during the day. There is a short period of variability due to clouds when the irradiance is two to three times within a few minutes.

4.3. Changes in Hydrochemical Parameters at the Studied Stations

AW entering the Arctic Ocean determines the heat balance [61], significantly changing the thermohaline structure of the waters. Thus, salty and denser waters are found above the desalinated PSW. AW brings nutrients to the Arctic [73]. In the Nansen Basin, the concentrations of inorganic nitrogen and phosphorus and dissolved silicon were significantly higher in AW than in PSW. The nutrients are transferred to the photic layer due to thermal convection. It is believed [74,75] that inorganic nitrogen is the main factor limiting phytoplankton growth.

At the MIZ stations (A and B), relatively high nitrogen concentrations were found in the layer close to the water surface. The nitrates concentration was sufficient to ensure phytoplankton growth [76,77]. In the surface waters of these stations, the silicon concentration is at a relative minimum (Table S3); therefore, the MIZ area's phytoplankton should be attributed to Si-limited. In open water, the thermocline formation and gradual deepening occur and, thus, the deepening of increased nutrient concentrations. Above the thermocline, the nitrogen concentration is at a relative minimum, decreasing to concentrations close to zero. Therefore, the state of phytoplankton is N-limited. This reason leads to oligotrophication, and the stratification of the water column plays the primary role here. This factor determines the PP in the open-water area, and the prediction of the strengthening of PP is associated with the dynamics of vertical transport.

4.4. Structure, Abundance and Biomass of Phytoplankton

In the high-latitude Arctic (80–83° N), the spring bloom of phytoplankton shifts to July–August. At the shelf and continental slope, the spring bloom is formed by neritic boreal-Arctic diatoms of the genus *Thalassiosira* belonging to the first-year ice flora [26,38,78], as well as species of the so-called “Atlantic community” [39]. Neritic species, such as diatom *Chaetoceros gelidis* and golden *Phaeocystis pouchettii*, form a spring bloom in the MIZ, usually in April, within the southern area of the Barents Sea Polar Front (BSPF) (80° N and 28° E), the so-called Atlantic side of the BSPF (Table 6) [39].

In the northern Barents Sea, the maximum level of phytoplankton biomass (up to 10 µg·L⁻¹ of chlorophyll concentration) is recorded in the surface water layer in the MIZ in August at the edge of the shelf [38]. *Gymnodinium* spp. and *Fragilariopsis oceanica* dominated, and the subdominants included *Thalassiosira* spp. and coccolithophore *Emiliania huxleyi*. Atlantic species of diatoms (*Rhizosolenia hebetata* f. *semispina*, *Chaetoceros decipiens*, *C. atlanticus* and *C. borealis*) were also detected in this area in the southern part of the Kvitøya Trench. In the Kvitøya Trench itself, according to data obtained in 1991 [39] and 2003 [38], phytoplankton biomass in open water was much lower. It did not exceed 4.0 µg·L⁻¹ of chlorophyll *a* (120 mg·m⁻³ of biomass). The main role in its formation was played by *Chaetoceros socialis* and *Phaeocystis pouchettii* (1991, July) and *Thalassiosira hyalina* and *C. socialis* (2003, August), i.e., species typical of spring bloom. It is characteristic that no oceanic Atlantic diatom species were observed in the Kvitøya Trench, which indicated a weak influence of AWBC.

Table 6. Time and place of sampling, dominant species according to literature and own data in the Nansen Basin and the northern part of the Barents Sea.

Authors	Time	Location	Ice	Dominant Species	Depth at Station
[26]	1984, August	82° N, 26° E	Multiyear, 3 m	<i>Melosira arctica</i>	≈2000 m
[37]	1984, August	82° N, 21° E	Multiyear, 4.5 m	<i>Melosira arctica</i>	≈2000 m
[37]	1988, September	80° N, 30° E	Second-year, 2.5–3 m	<i>Thalassiosira bioculata</i>	≈1000 m
[39]	1991, July	81° N, 30–31° E	Multiyear, 2–3 m	<i>Fragilariopsis cylindrus</i> , <i>T. bioculata</i> , <i>M. arctica</i>	≈1000 m
[39]	1991, July	80° N, 29–30° E	MIZ, 2–3 m	<i>P. pauchetii</i> , <i>C. jellidii</i> , <i>T. antarctica</i> , <i>T. bioculata</i> , <i>T. borealis</i> , <i>T. nordensk</i>	500 m, Kvitøya
[78]	1996, August	82° N, 33° E	Multiyear, 3–4 m	<i>T. bioculata</i>	700 m
[78]	1996, August	81° N, 33° E	Multiyear, 3–4 m	<i>T. bioculata</i>	200 m
[38]	2003, August	80° N, 30° E	open water	<i>Fragilariopsis oceanica</i> , <i>E. huxleyi</i> , <i>Gymnodinium</i> spp., <i>Thalassiosira</i> spp.	500 m
[41]	2012, July August	83° N, 20° E	Multi-year	<i>Geterothrophic dinoflagellates</i> , <i>Small flagellates</i>	3000 m
[41]	2013, July	83° N, 21° E		<i>Fr. oceanica</i> , <i>P. pouchetii</i> , <i>T. bioculata</i> (15 m)	>1000 m
Our data	2020, August	83°16' N, 38°14' E	MIZ	<i>Porosira glacialis</i>	3703 m
Our data	2020, August	83°04' N, 34°34' E	MIZ	<i>Porosira glacialis</i>	3670 m
Our data	2020, August	82°15' N, 36°32' E	open water	<i>Thalassiosira</i> spp., <i>Eucampia groenlandica</i> , <i>P. pouchetii</i> , <i>E. huxleyi</i>	2162 m

We analyzed the summer data of other researchers from 81 to 83 north of Svalbard, including the Ermak plateau (Table 6) [27,38,40]. It can be noted that from 1984 to 2012, there was almost always an ice cover of different ages with a characteristic composition of phytoplankton. At the northernmost deep-water stations, A and B, located in the MIZ, early stages of phytoplankton succession were noted: (i) the stage before bloom (Station B) and (ii) the stage of bloom (Station A). Here, the bulk of phytoplankton was located in the upper 10 m water layer above a sharp gradient halocline separating melted water from the underlying AW. The pre-bloom stage was characterized by small phytoplankton biomass. However, a high concentration of nutrients in the upper 10 m layer and a high level of PP indicated a high potential of the community. Bloom in the MIZ at station A was characterized by an extremely high phytoplankton biomass ($30.0 \text{ g} \cdot \text{m}^{-3}$), a high concentration of chlorophyll *a* ($13.1 \mu\text{g} \cdot \text{L}^{-1}$) (Figure 4), and a high level of PP ($64 \text{ mg} \cdot \text{C} \cdot \text{m}^{-3} \cdot \text{day}^{-1}$). The integral PP for the euphotic zone was $462 \text{ mg C m}^{-2} \text{ day}^{-1}$. For comparison, in August 2020, much to the south (70° N, 39° E) in the Barents Sea during the intense bloom of coccolithophorid *Emiliania huxleyi*, the maximum value of PP was $148 \text{ mg C m}^{-2} \text{ day}^{-1}$.

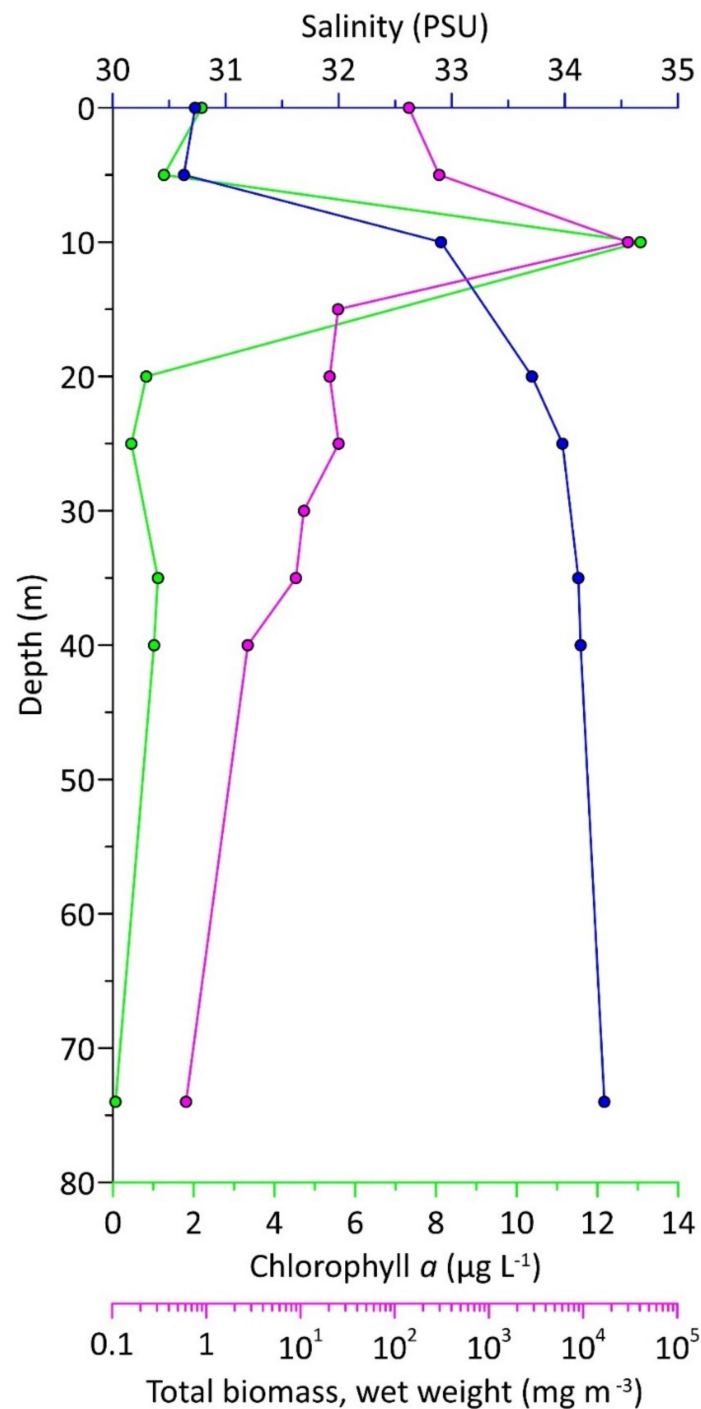


Figure 4. Change in salinity, chlorophyll, and wet weight biomass concentration with depth at station A.

The dominant species, large centric boreal-Arctic diatom *Porosira glacialis*, is associated with the first-year ice [26]. This species was discovered for the first time in the high-latitude Arctic due to the extraordinary event of monospecific intensive growth. Since the studied sites were located close to the ice edge formed by the multiyear sea ice, the multiyear ice flora species were also present in the surface 20 m desalinated water layer. The subdominants of the phytoplankton community were represented by neritic boreal-Arctic diatom species typical for first-year ice as well as boreal species of the “Atlantic community” [39] forming spring blooms on the shelf, including the Atlantic area of the BSPF. The presence of large Atlantic diatoms of the genus *Chaetoceros* and *Rhizosolenia*, and

Sundstroemia setigera in the phytoplankton of the deep-water sites and the high level of similarity of the phytoplankton species composition at these stations with station C located in the AWBC may indicate the transfer of the Atlantic flora, the first-year ice flora, and *P. glacialis*—the main dominant species in the MIZ in the summer of 2020.

Thus, in the Nansen Basin, representatives of various ecosystems are revealed in the photic water layer, which can serve as a seed for intensive growth. Does only one species of large diatom, *Porosira glacialis*, have an advantage under these conditions? The intensive growth of *P. glacialis* occurred on a sharp salinity gradient associated with the halocline between the surface melting water and the underlying polar water. Thermal vertical convection, moving upward from the core of AW, brings Atlantic species to the photic layer and enriches the halocline zone with nutrients. At stations A and B, relatively high silicon concentrations (more than 1 μM) can sustain diatoms' active growth [79,80]. At station B, a nitrogen concentration that does not limit the growth of phytoplankton was detected at the layer of 9 m. At station A, a similar concentration was measured a little deeper (Table S3). The phosphorus concentrations are high in the upper water layer, which causes a low molar ratio of nitrogen to phosphorus. Relatively high dissolved silicon and nitrogen concentrations contribute to the growth of small diatoms, which occurs during the spring bloom in the North Atlantic [81] and the Barents Sea [82].

Given that the position of the halocline changes over time, the concentration of nutrients at a certain depth becomes a dynamic characteristic. In addition, the incident light also changes significantly over time. The amplitude of variations depends not only on the changing of clouds and the angle of sun inclination but also on the significant upward movement of the halocline base. In such dynamic conditions, large diatoms gain an advantage, which can change the specific absorption coefficient of chlorophyll and accumulate nutrients [68]. Two mechanisms can explain the difference in *P. glacialis* biomass at stations A and B. The first hypothesis is that at station B, the biomass of this species is low since this is the initial phase of bloom; by analogy with a batch culture, this is the phase of exponential growth, and at station A, the stationary phase. Very high rates of photosynthesis support this hypothesis at station B ($30.6 \text{ mg} \cdot \text{C} \cdot \text{m}^{-3} \cdot \text{day}^{-1}$, $256 \text{ mg} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$). The second hypothesis is that the eddy may move the halocline close to the water surface [60], and phytoplankton can get to the zone of photoinhibition (see Table 5). In this case, large cells gain an advantage due to lower values of specific light absorption coefficient compared with small cells gaining an advantage due to the packing effect [57,83–85]. This ability allows large cells to protect themselves from photodamage and, as a result, prevents the energy costs for recovery [86]. Additional advantages are provided by the ability of cells to rapidly change the specific light absorption coefficient due to the movement of chloroplasts [67].

It is also possible that halocline plays the role of a filter on which large cells settle due to the low g C: cell-volume ratio [87]. Smaller and denser cells pass through this filter.

Such a physicochemical structuring of the community towards the dominance of large diatoms does not mean that secondary producers do not affect the level of biomass and the structure of phytoplankton [88,89], but implies that such a shift in the size structure will affect the formation of the species composition of zooplankton [90].

A later stage of phytoplankton succession, the so-called “post-bloom stage”, was noted and revealed at station C, located in the AW boundary current passage zone. The characteristic of this stage was the deep maxima of phytoplankton biomass (Table 6), formed by the spring bloom species deposited in the nutricline. At station C, the structure of phytoplankton was characteristic of shelf waters north of Svalbard (Table 6). In the upper 20 m layer, dinoflagellates dominated. Deeper, in the Arctic water masses, a deep maximum was recorded, consisting of neritic algae of spring bloom, belonging to the first-year ice flora x and the bloom of Atlantic species in the open water (*Eucampia groenlandica*). Bloom of *Phaeocystis pouchettii* was observed at a depth of 38 m near the boundary of the photic zone because this species has a high specific light absorption coefficient (Table 6).

Atlantic species *Emiliania huxleyi* was observed in maximum abundance at the lower boundary of AW at a depth of 602 m and a depth of 10 m above the seasonal thermocline.

Atlantic species enter the high-latitude Arctic waters due to the North Atlantic Current and the warmer surface Norwegian current (both currents form the West Svalbard Current). Probably, the hydrophysical structure of the research area can explain this coccolithophore vertical distribution.

A deep biomass maximum was observed at the edge of the shelf (stations D and E) (Tables 5, 6 and S4). The greatest similarity in the structure of the leading phytoplankton complex was distinguished at stations D and C. At both D and F stations, the cold-water species *Monochrysis* sp. was also dominant. At station F, located in the southern Franz Victoria Trench, over 60% of the total biomass comprised *Porosira glacialis*. If we consider that this alga's spores and vegetative cells are marked in the core of AW at stations C and A, then it can be assumed that *P. glacialis* was transported to the deep Arctic Basin by the AW. The formation of the first-year sea ice in the Nansen Basin starts in January [43]; before that time, intense winter convection can contribute to the transfer of spores of this species into the upper water layer and their freezing into the bottom of the first-year ice cover. Once summer arrives, most of this first-year ice quickly melts, and spores of *P. glacialis* enter the photic zone enriched with nutrients, which explains an intensive bloom of these diatom species.

The phytoplankton structure of the northern Barents Sea shelf changes due to the greater warming of the surface water layer; the seasonal thermocline is buried up to 20–30 m, and the complete exhaustion of nitrates in the upper layer leads to a reduction of the autotrophic (diatom) component of the community. The post-bloom stage is observed in the community with the dominance of cold-water golden algae of the genus *Monochrysis* and dinoflagellates. At stations F and G, located in the Franz Victoria Trough, in comparison with other stations, oceanic Atlantic diatom species were practically absent (Table S4). Other researchers also pointed this out in the Kvitøya Trench of the Barents Sea [38]. However, the presence of coccolithophore *Emiliania huxleyi* in a 20 m surface water layer at station F and another indicator of Atlantic warm-water species *Triplos horridus* suggest that AW enters the trench in two ways, including the upper water layer.

It should be noted, however, that such a pattern is not always observed. For example, at the beginning of August 2017, deep phytoplankton maximum (from 1.0 to 5.0 g·m⁻³) was observed in the Franz Victoria Trench and the waters known as the polynya south of Franz Josef Land and the polynya south of the Kvitøya Trench (77–79° N), formed by both diatoms' species of the first-year ice of genus *Thalassiosira* and Atlantic neritic diatom *Eucampia groenlandica* [40]. The presence of oceanic Atlantic diatoms species associated with AWBC at all studied sites suggests that the periodic increase of PP in the northern part of the Barents Sea is directly related to the upwelling of AW.

5. Conclusions

A unique set of field data on the summer phytoplankton of the deep-water part of the Nansen Basin and the adjacent northern shelf of the Barents Sea has been obtained. The two northernmost stations (83° N) were in the MIZ area; the rest were in open water. The presence of mPSW, PSW, and AW was characteristic of the MIZ; there are only two water masses in open water, namely PSW and AW, and at the southernmost station, the contribution of AW was minimal. In the MIZ, the first-year ice, multiyear ice, and Atlantic species were noted. Atlantic species and first-year ice species were found in open water: in the deep-water part of the Nansen basin, the multiyear ice was replaced by the first-year one. Only first-year and multiyear ice floras were present at the southernmost station. Furthermore, intensive growth (up to 30.0 g·m⁻³) of the large centric diatom *Porosira glacialis* was found in the MIZ area. The dominance of this species and such biomass in the MIZ was discovered for the first time. This result is unexpected since it is well known that the intensive growth of diatoms with smaller cell sizes as species of the multiyear ice is expected in the high latitudes of the Arctic.

The main feature of this high biomass is that it was located on the halocline between mPSW and PSW. It was previously assumed that there was an increase in the PP of phyto-

plankton in open water compared with the community under sea ice due to a sharp increase in light intensity. However, in our case, this effect of increased silicon concentrations is due to increased vertical nutrient fluxes caused by shallowing of the AW. The light intensity does not limit the growth of phytoplankton but is close to optimal or even photoinhibition PP. A thermocline formed in open water has created a strong stratification limiting the vertical nutrient fluxes. Above the thermocline, the nitrogen concentration becomes the factor limiting growth. Therefore, the maxima of phytoplankton biomass are connected by a thermocline and formed by non-Arctic Atlantic species in association with species of the first-year ice. A decrease in phytoplankton biomass is observed in the zone of weak influence or complete absence of AW; here, the species of ice flora determine phytoplankton composition. A silicon-limited state of phytoplankton is observed in the MIZ area, and a transition to a nitrogen-limited state is noted in open water. The hypothesis of an increase in ocean productivity with an increase in open water due to a reduction in the area of ice cover is not apparent.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse11020453/s1>, Figure S1: PAR values along the R/V track. The red line shows the estimated values for the case of a cloudless sky. August 16–17, 2020; Table S1: The location of stations, time of sampling, depth of the thermocline, the halocline and the pycnocline.; Table S2: Temperature, salinity and density at mPSW, at the score of PSW and AW and the depth where temperature equal 0 and 1 °C at all sampling station; Table S3: The concentration of silicates, phosphates and nitrates at various depths at all the stations studied; Table S4: Total biomass of the phytoplankton, temperature and salinity at sampling stations in the Nansen Basin and the Barents Sea in August 2020; Table S5: Maximal phytoplankton biomass, temperature, salinity, nutrients concentrations and dominant species.

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