

Article

Summer Phytoplankton Communities Across Contrasting Water Masses in the Fram Strait

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Abstract

In the Fram Strait, Atlantic Water (AW) flows northward through the eastern part of the strait, while Polar Surface Water (PSW) moves southward from the Arctic Ocean through its western part. Mixing of these water masses produces mixed AW (mAW). As these water masses move, significant changes occur in salinity, temperature, density, and nutrient concentrations, restructuring the phytoplankton community. Based on surveys conducted in August 2021 during the 84th cruise of the R/V *Akademik Mstislav Keldysh*, the dominant species were identified for each water mass. Among the key species (10 diatoms, 11 dinoflagellates, two coccolithophores, and one species each of chrysophyte, haptophyte, and ciliates), three ecological assemblages were distinguished: a cold-water PSW indicator complex (*Porosira glacialis* and *Rhizosolenia hebetata* f. *hebetata* among diatoms, the dinoflagellate *Protoperidinium islandicum*, and the ciliate *Mesodinium rubrum*); a warm-water AW complex (*Navicula planamembranacea*, *Stephanopyxis turris*, *Rhizosolenia styliformis*, the dinoflagellates *Protoperidinium depressum* and *Tripes* spp., and the coccolithophore *Coccolithus pelagicus*); and an mAW complex (the diatom *Thalassiosira rotula*, the coccolithophore *Gephyrocapsa huxleyi*, the haptophyte *Phaeocystis pouchetii*, and the chrysophyte *Monochrysis* sp.). Moving from south to north into the Fram Strait and from east to west towards the Greenland shelf, warm-water Atlantic indicator species were first replaced by mAW species, and then by cold-water species in the PSW. Maximum phytoplankton biomasses (up to 670.8 mg/m³) were observed in the marginal ice zone, driven by the intensive growth of large diatoms at depths within the euphotic zone where AW and PSW interact. If this interaction depth lies outside the euphotic zone, the phytoplankton biomass is determined by ciliates. In open water, large dinoflagellates contributed most to the biomass, indicating the decisive role of mixoplankton (mixotrophic plankton) in summer at high Arctic latitudes.

Keywords: arctic ocean; Fram strait; Atlantic water; polar surface water; phytoplankton; diatoms; dinoflagellates



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1. Introduction

Climate change is leading to significant transformations of ecological systems, which can have serious economic consequences. The most sensitive region is the Arctic [1,2], where recent climatic shifts have resulted in a sharp reduction in ice cover area [3,4]. Simultaneously, the structure of the ice is changing; it is becoming thinner, and ultimately, multi-year ice is being replaced by first-year ice [5]. Calculations indicate that if the

current trend continues, the Arctic Ocean is projected to become ice-free in summer, with ice cover restricted to winter [6,7]. The primary cause of such profound changes in the western Eurasian Arctic is believed to be the intensity of the inflow of warm and saline Atlantic Water (AW) [8–11]. As it moves northward, AW meets the Polar Surface Water (PSW) and subducts beneath it, creating a complex hydrographic structure [12]. The presence of warm water above cold water promotes the development of convection. The intensity of vertical heat transfer determines the dynamics of the ice cover. The halocline, located between the PSW and AW, plays a particular role in heat transfer; its thickness regulates density stratification and, consequently, is a crucial climate-regulating factor [8]. Weakening of the vertical density stratification increases the intensity of convection, as observed during winter in the Nansen Basin [13]. This results in a reduced rate of ice formation in winter and changes in its characteristics, such as thickness and physical structure. Changes in ice thickness led to alterations in the light regime under the ice [14,15], primarily an increase in photosynthetically active radiation (PAR) to levels sufficient to initiate phytoplankton blooms under the ice. Under-ice blooms contribute significantly to increasing the productivity of the pelagic ecosystem in the Arctic region [16–20].

In the Eurasian Arctic, warm Atlantic Water enters the Arctic Ocean mainly through the Fram Strait and the Barents Sea. In the Barents Sea, the increased influence of AW on hydrography and ecosystem structure is well studied [21]. This phenomenon, termed Atlantification [8,9], leads to changes in phytoplankton structure with the replacement of local species by Atlantic ones, shifts in seasonal dynamics and phenology of phytoplankton blooms, and restructuring of the entire food web [22–31]. These shifts will alter the biogeochemistry of the existing ecosystem [32].

A fundamental characteristic of marine ecosystems at high latitudes is pronounced seasonality, involving a transition from the polar night in winter to round-the-clock insolation in summer. A distinct light regime characterizes this region [33], shaped by seasonal variations and the vertical distribution of light under ice and in open water [34]. In open water, a transition occurs from a light-limited ecosystem to a nutrient-limited one [35]. This shift is thought to enhance the productivity of the pelagic ecosystem. This inference is based on the concept of light limitation of phytoplankton growth under ice [36–38].

Through the eastern part of the strait, the West Spitsbergen Current (WSC) carries warm and saline Atlantic Water (AW) from south to north. In the western part of the strait, the East Greenland Current (EGC) transports cold and less saline Arctic water in the opposite direction. A complex horizontal structure forms in the strait, including AW recirculation loops, most pronounced around 79° N, and eddies [39–41]. The temperature of AW in the WSC is believed to be increasing [42,43], while estimates of the water volume transported through the Fram Strait are contradictory. Some researchers suggest it does not change over time [42], whereas others report an upward trend [44]. Challet et al. [45] propose that the anomalously high water temperature in the Fram Strait is also linked to a weakening of the westward flow of colder polar water from the northern Barents Sea towards Svalbard.

The study of phytoplankton in the North Atlantic, particularly in the Fram Strait, began in the mid-20th century [46,47]. Subsequent studies have shown a tendency towards increasing chlorophyll-a concentration in the WSC, while no similar trend is found in the EGC waters [24]. Interannual variability in phytoplankton composition in the Fram Strait, as well as significant differences in composition and size structure between AW and PSW, have been documented [24,48,49].

As the AW flow moves northward, its heat content, salinity, and density change [12,42]. Climatic changes, in turn, facilitate the northward expansion of boreal species [22,50–53]. However, meridional changes in environmental conditions and interactions with PSW

and its characteristic species introduce uncertainty into predictions of phytoplankton composition. Meandering of the WSC, recirculation loops, and eddies further contribute to the complex spatiotemporal distribution of phytoplankton during the seasonal northward retreat of the ice edge. The southward-flowing EGC modifies its physicochemical properties and, consequently, its phytoplankton composition as it moves from north to south.

The northward movement of the ice edge and its interannual variability pose challenges for the operational assessment of phytoplankton composition and productivity. Key operational methods include remote sensing of the ocean surface, which has both strengths and limitations. Remote sensing measures sea surface temperature (SST) most accurately, so it is important to relate phytoplankton composition to this readily determined factor. Conversely, phytoplankton composition serves as an indicator of water masses [54,55], which are characterized by parameters such as temperature and salinity [56–59]. A general biogeographic pattern is the increasing dominance of diatoms from the equator toward the poles [60]. Therefore, diatoms are expected to be the dominant phytoplankton group at high latitudes. Indeed, under-ice phytoplankton blooms consist of pennate diatoms [19]. However, a spring bloom under the ice caused by the ciliate *Mesodinium rubrum* has also been observed [61]. Spring blooms in open waters at high latitudes are typically driven by small pennate and centric diatoms or the haptophyte *Phaeocystis pouchetii* [29,30,62,63]. Either diatoms or *P. pouchetii* can be the dominant group in the open waters of the Fram Strait [24,64]. In the Nansen Basin, within the marginal ice zone (MIZ) and the halocline layer, an intense bloom of the large diatom *Porosira glacialis* was recorded [65]. Thus, the ecosystem exhibits a variety of responses in terms of dominant phytoplankton species, and identifying the main factors regulating the structure of the high-latitude phytoplankton community during summer is not a trivial task. A natural hypothesis is that the species composition is determined by water mass characteristics—in other words, by the hydrography of the region. However, for the Fram Strait, it remains unclear how the movement of water masses, their interaction, and the associated transformation of environmental conditions determine the spatiotemporal patterns of phytoplankton composition, abundance, and biomass distribution.

The aim of this study was to trace the changes in phytoplankton composition, abundance, and biomass during northward transport through the Fram Strait and to understand the processes shaping the community structure in different water masses. The following hypotheses were tested:

- Water masses are characterized by specific dominant species;
- As water masses move northward, their physicochemical properties change, leading to transformations in phytoplankton composition;
- In the MIZ, a two-layer vertical structure develops, wherein Arctic species dominate in the upper layers and Atlantic species dominate in the lower layers;
- Highly productive zones develop within the euphotic zone at the boundary where PSW and AW interact.

Testing these hypotheses allows the identification of indicator species of water masses and currents in the Fram Strait, which is important for predicting the ongoing Atlantification of the Arctic Ocean. To achieve this goal and test the validity of the hypotheses, the following tasks were carried out during the cruise of the R/V Akademik Mstislav Keldysh in the summer of 2021: (i) identification of water masses and investigation of the physical and optical properties of water and nutrient concentrations; (ii) study of the species composition, abundance, and biomass of dominant phytoplankton species in AW and PSW and during their interaction; (iii) assessment of the potential use of individual phytoplankton species as indicators of different water masses.

2. Methods

2.1. Study Area

The research was conducted in the first half of August 2021 during the 84th cruise of the R/V Akademik Mstislav Keldysh. Sampling was carried out along four transects (Figure 1). Transect 1 extended across the Fram Strait region from the Barents Sea shelf in the east to the Greenland shelf in the west at 74–76° N (stations 7045–7052; Figure 1, Table S1). Transect 2 was located off the southern tip of Svalbard (stations 7063–7065). Transect 3 spanned the Fram Strait, extending from the western coast of Svalbard to the ice edge in the northern part of the strait (stations 7066–7081). Transect 4 was located in the deep-water Nansen Basin and ran in a meridional direction from the shelf break in the south to the ice edge in the north (stations 7069–7078). Additionally, two stations were positioned in the drift ice zone (stations 7075 and 7076), and another two were located at the ice edge near the Yermak Plateau (stations 7079 and 7080).

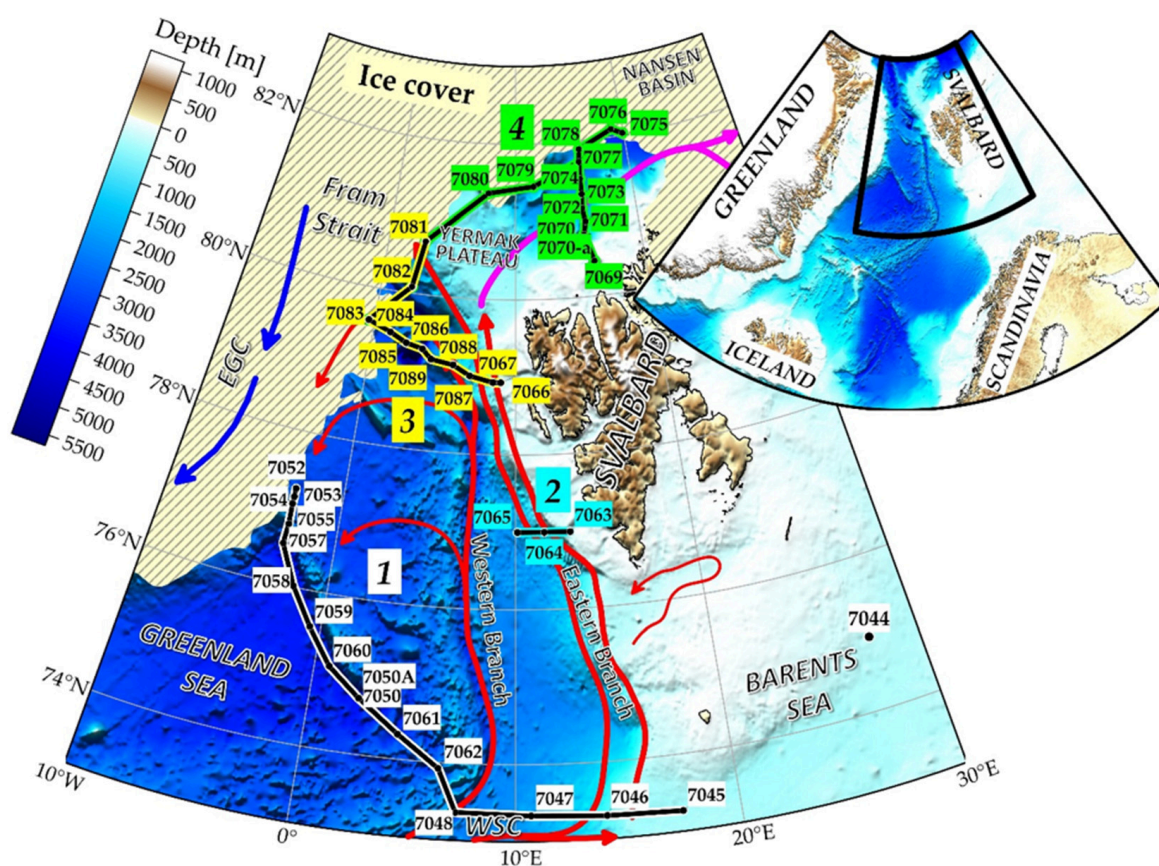


Figure 1. Map of sampling stations from the 2021 cruise. The scheme of currents is adapted from Walczowski [39]. Red arrows indicate the West Spitsbergen Current (WSC) and its Western and Eastern branches. Bathymetry is based on GEBCO data (<https://www.gebco.net>, accessed on 20 April 2021). Numbers 1–4 denote the transects. Ice cover images are composites for 2–18 August 2021, provided by the Norwegian Meteorological Institute (<https://cryo.met.no>, accessed on 29 August 2021).

2.2. CTD Data and Sampling

Hydrographic data and water samples were collected using an SBE 911plus CTD system (Sea-Bird Electronics, Inc., Bellevue, WA, USA) coupled with an SBE 32 Carousel Water Sampler equipped with 10 L Niskin bottles. The CTD unit was equipped with sensors for temperature (accuracy ± 0.001 °C), conductivity/salinity (accuracy ± 0.001), and

pressure (accuracy $\pm 0.001\%$ of full scale). Vertical profiles of temperature and conductivity were obtained at each station from the surface to near the seafloor.

Sampling depths were determined based on real-time analysis of CTD profiles (temperature, salinity, density), fluorescence data and photosynthetically active radiation (PAR), with a focus on the euphotic zone. Typically, at least five samples were collected within the euphotic layer at each station. In total, 249 water samples were collected for phytoplankton and nutrient analyses from the same Niskin bottle casts. Based on the CTD data, the thickness of the upper mixed layer (UML) was estimated.

Phytoplankton samples were preserved with neutralized formaldehyde to a final concentration of 0.8–1.0%. This reduced concentration, compared with the standard 4%, was chosen because the samples were not intended for long-term storage. Processing was carried out within two to three months after collection, during which mild fixation ensured better preservation of cell morphology. The samples were stored in the dark at room temperature and subsequently concentrated by slow sedimentation and decantation.

2.3. Species Identification, Cell Counting, and Biomass Estimation

Species identification was based on morphological features, following Tomas et al. [66], Throndsen et al. [67], and the World Register of Marine Species (WoRMS; <https://www.marinespecies.org>, accessed on 26 January 2026). Cells were identified and enumerated using an Ergaval light microscope (Carl Zeiss, Jena, Germany) at magnifications of $160\times$ and $640\times$.

Cells with linear dimensions $< 20\ \mu\text{m}$ were counted in a 0.05 mL Nageotte chamber, whereas larger cells were enumerated in a 1 mL Naumann-type nanoplankton chamber. Unidentified cells measuring 4–10 μm were classified as “small flagellates.” Cells $< 2\ \mu\text{m}$ were excluded from total phytoplankton biomass estimates. Cell biovolume and biomass were calculated according to Hillebrand et al. [68]. Wet biomass was converted to carbon content using allometric equations [69]. A species was considered dominant if it contributed more than 50% of the total phytoplankton biomass.

2.4. Nutrient Analyses

Analyses of phosphate phosphorus ($\text{PO}_4\text{-P}$), dissolved silicate ($\text{SiO}_4\text{-Si}$), nitrate ($\text{NO}_3\text{-N}$), nitrite ($\text{NO}_2\text{-N}$), and ammonia ($\text{NH}_4\text{-N}$) were performed using a segmented continuous-flow Technicon II autoanalyzer and/or colorimetric methods [70,71]. Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite, and ammonia. The nutricline depth was defined as the depth at which both dissolved silicate and DIN concentrations equal $1\ \mu\text{M}$ [72].

2.5. Optical Measurements

Underwater PAR (400–700 nm) was measured using an LI-192 quantum sensor, while surface incident irradiance was measured concurrently with an LI-190C quantum sensor (LI-COR Environmental, Lincoln, NE, USA) mounted on the ship’s deck and positioned to avoid shading by the superstructure. Continuous profiling of the beam attenuation coefficient ($\text{BAC}, \text{m}^{-1}$) was performed using a compact PUM-A transmissometer [73]. BAC represents the sum of the total absorption and total scattering coefficients [74] and is used to characterize the optical properties of the water column. The euphotic depth was defined as the depth at which irradiance decreased to 1% of the surface value; the depth of the 0.1% light level was also determined.

2.6. Ice Cover

The ice cover image is a composite for the period 16–18 August 2021, provided by the Arctic and Antarctic Research Institute (AARI; https://data.aari.ru/odata/_d0015.php,

accessed 18 August 2021). The marginal ice zone (MIZ) was defined as the area where sea ice concentration ranges between 15% and 80% [75].

2.7. Statistical Analyses

A significance level of 5% was adopted for all statistical tests. Differences in community composition among water masses were assessed using PERMANOVA (permutational multivariate analysis of variance) with 9999 permutations. Species contributing most to the dissimilarities among water masses were identified using SIMPER (similarity percentage) analysis. Indicator species for each water mass were identified using the IndVal method [76]. Analysis of variance (ANOVA) was used to test for significant differences between samples, and post hoc pairwise comparisons were performed using *t*-tests. Pairwise Pearson correlation coefficients were calculated between water parameters and environmental variables. All statistical analyses were performed using PAST version 4.13 (<https://www.nhm.uio.no/english/research/resources/past/>, accessed 15 May 2026).

3. Results

3.1. Ice Cover

In August 2021, persistent ice cover was observed north of 82° N and east of 20° E. Only a small portion of the Nansen Basin was ice-free (Figure 1). West of this longitude, the ice edge extended further south, reaching approximately 0° W at 80° N. South of this latitude, the ice boundary continued southward beyond this longitude, approaching 3° W at 76° N.

3.2. Water Masses and Vertical Structure of the Water Column

Water masses were identified following the terminology proposed by Pérez-Hernández et al. [57]. Additional studies were also consulted to delineate water mass boundaries [58,59]. In the present study, Atlantic Water (AW) is defined by salinity > 34.75 and potential temperature > 1.544 °C (Tables 1 and S2, Figures 2–6). Mixing with colder and fresher PSW results in the transformation of AW, forming mAW, with salinities ranging from 34.0 to 34.75. The cold, fresh Arctic waters of the PSW are typically located above the AW; their salinity ranges from 31.30 to 34.0, and their temperature is below 0 °C. During ice melt, a meltwater layer (mPSW) forms at the surface, characterized by salinity < 31.28 and temperature below 0 °C. This surface layer of mPSW is typically thin and overlies the halocline, a layer characterized by a rapid change in salinity with depth. In summer, atmospheric heating leads to the formation of a warm surface layer of Arctic water with temperatures above 0 °C, designated as PSWw. Consequently, a thermocline develops, the depth of which varies depending on local hydrographic conditions.

Table 1. Changes in temperature, salinity, and density in the core of AW and PSW, as well as the minimum temperature in mPSW and maximum temperature in PSWw at the stations of the studied area. ϑ : potential temperature; S: salinity; σ : density.

Water Mass	Potential Temperature (ϑ), °C	Salinity (S)	Density (σ), kg m ^{−3}
AW	$\vartheta > 1.544$	$34.75 < S < 35.03$	$27.80 < \sigma < 27.9$
mAW	$\vartheta < 4.1$	$34.0 < S < 34.75$	$26.9 < \sigma$
PSW	$-1.659 < \vartheta < 3.0$	$31.30 < S < 34.0$	$25.16 < \sigma < 27.68$
mPSW	$-1.67 < \vartheta < 0$	$30.85 < S < 31.28$	$24.3 < \sigma < 25.7$
PSWw	$0 < \vartheta < 3.0$	$31.04 < S < 33.9$	$25.6 < \sigma < 27.27$

Analysis of T-S curves revealed a distinct vertical and meridional separation of water masses (Figure S1). AW was present at all stations. In the southeastern part of the study

area, it occupied the entire euphotic zone, whereas further north and west, it was found beneath the PSW.

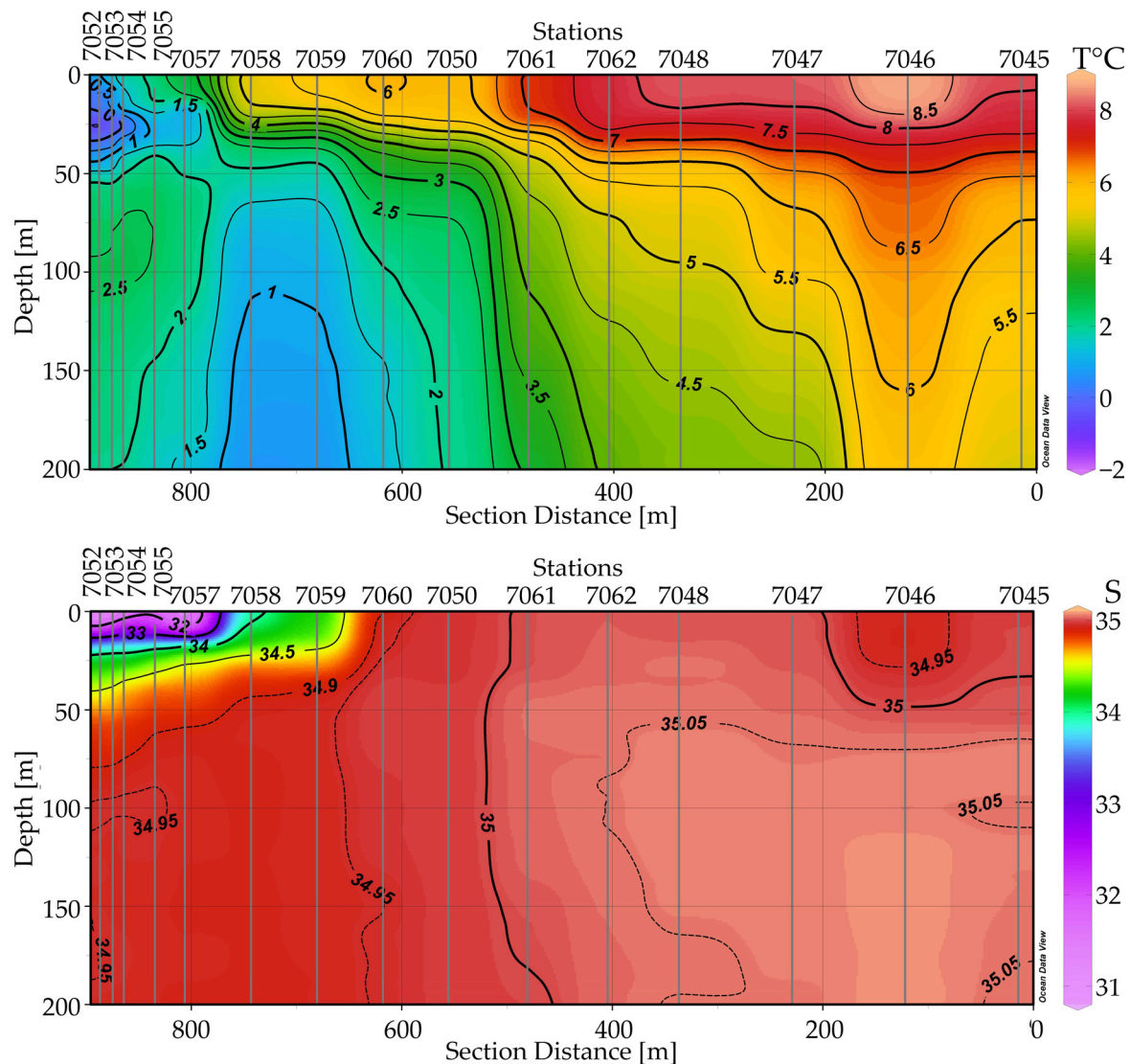


Figure 2. The temperature and salinity of the water column in Transect 1.

Sea surface temperature exhibited distinct meridional and zonal gradients, varying considerably from positive values in the south and east to negative values further north and west (Figures 2–6, Table S2). Salinity showed similar spatial patterns.

The halocline between mPSW and PSW was located close to the surface and was typically sharp (Figures 2–6, Table S2). Within the AW layer, the halocline was weak and often situated below the euphotic zone. A second halocline, observed between PSW and AW, was also typically located beneath the euphotic zone. The depth of the halocline (when present) varied considerably across stations. This depth increased with water temperature ($r = 0.51$, $p = 0.002$). In PSW, the halocline depth varied over a narrower range (up to 21.4 m) and increased with salinity ($r = 0.66$, $p = 0.001$).

3.2.1. Transect 1

Along Transect 1, two distinct regions were identified: the Atlantic and the Arctic regions. The Atlantic region, located in the eastern part of the transect and bounded by the eastern and western branches of the WSC, was characterized by the highest values of water temperature and salinity (Table S2; Figures 2 and S1). In the Arctic region, which includes

the large-scale cyclonic circulation of the Greenland Sea, temperature and salinity in the upper 50 m productive surface layer decreased from east to west toward the Greenland shelf. At the surface (Station 7050), salinity was 35.0 and temperature 5.8 °C, whereas near the Greenland shelf (Station 7052), salinity dropped to 31.0 and temperature to 0.41 °C.

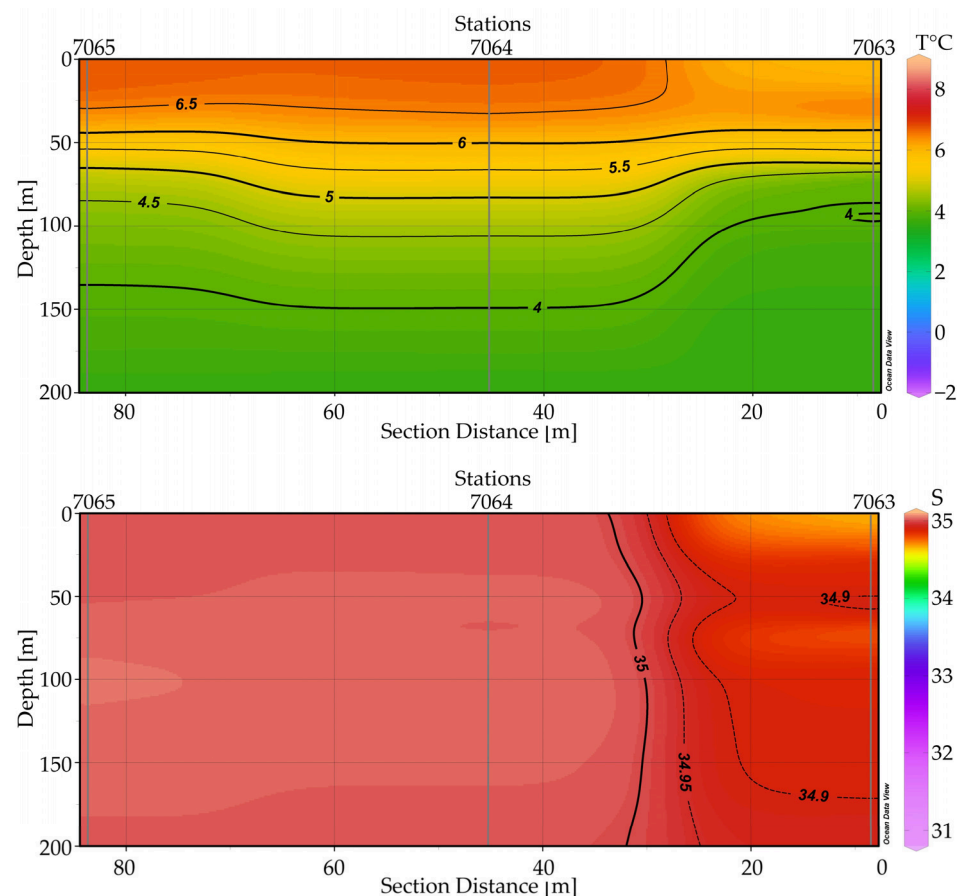


Figure 3. The temperature and salinity of the water column in Transect 2.

Sea surface temperatures (SST) in the AW were high, and the vertical temperature distribution was characterized by a thermocline at depths of 20–50 m (Figure 2 and Table S2). In most of the Polar Surface Water (PSW), temperatures declined sharply but did not reach negative values. However, at stations 7052–7054, a layer of PSW with negative temperatures was observed at depths of 25–27 m.

Surface salinity at the eastern stations consistently matched that of AW, whereas at western stations 7052–7058 it was characteristic of PSW (Figures 2 and S1 and Table S2). Regarding the vertical salinity distribution, no significant salinity gradients were observed in the AW up to Station 7050. In the PSW, at stations 7052 and 7053, the halocline was situated at a depth of 12–13 m; at Station 7054, it was located close to the surface.

3.2.2. Transect 2

Based on physical parameters, the offshore part of the transect belonged to the AW domain, while shelf Station 7063 was influenced by the cold Sørkapp Coastal Current. The cold coastal waters and warm AW formed a distinctive vertical structure: less saline and colder waters (temperature ~6 °C) were located at the surface, whereas temperature and salinity increased with depth (Table S2; Figure 3). At a depth of 32 m, the highest temperature and salinity, characteristic of AW, were observed. At stations 7064–7065, AW was also recorded at the surface.

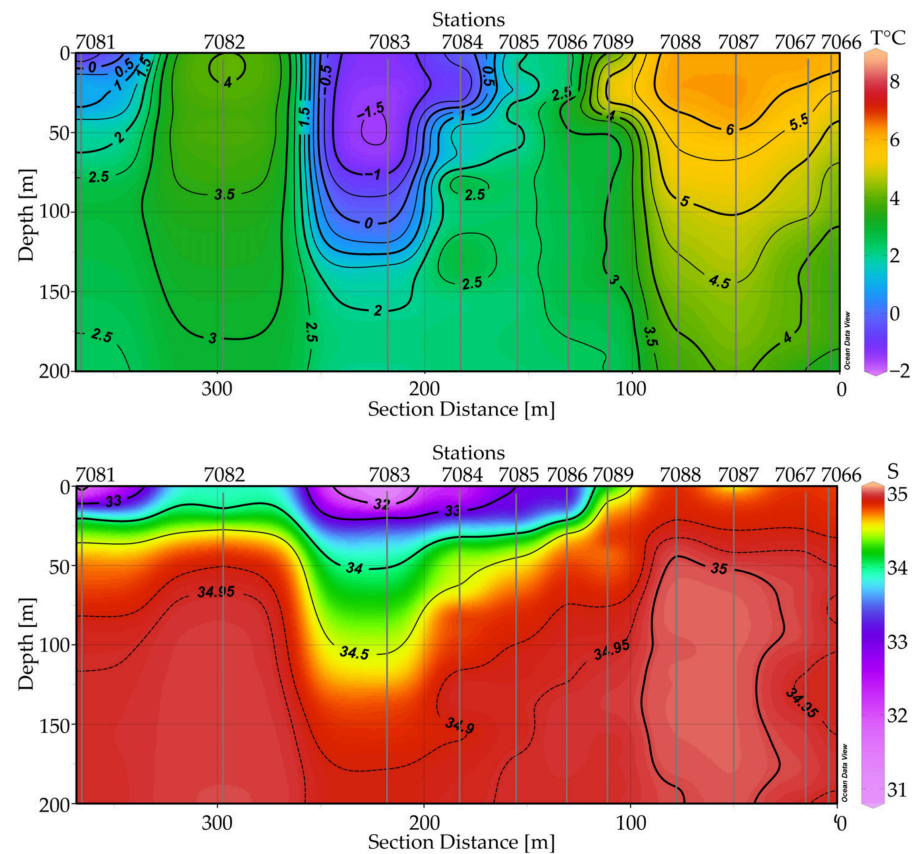


Figure 4. The temperature and salinity of the water column in Transect 3.

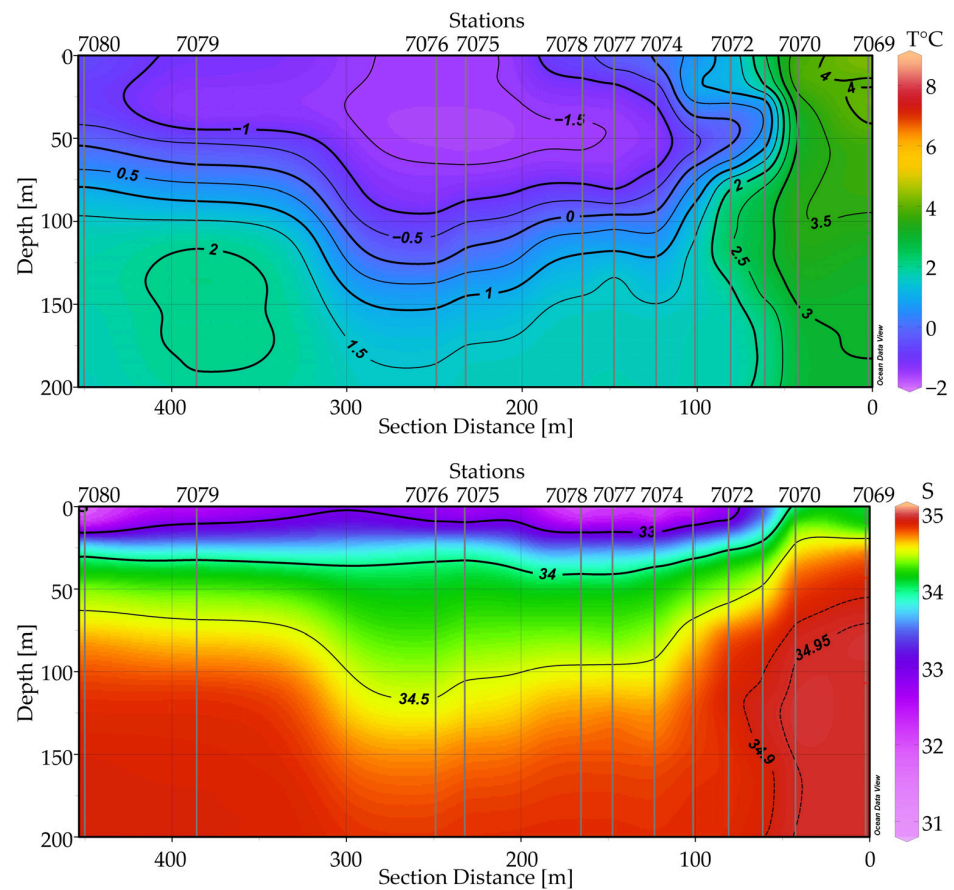


Figure 5. The temperature and salinity of the water column in Transect 4.

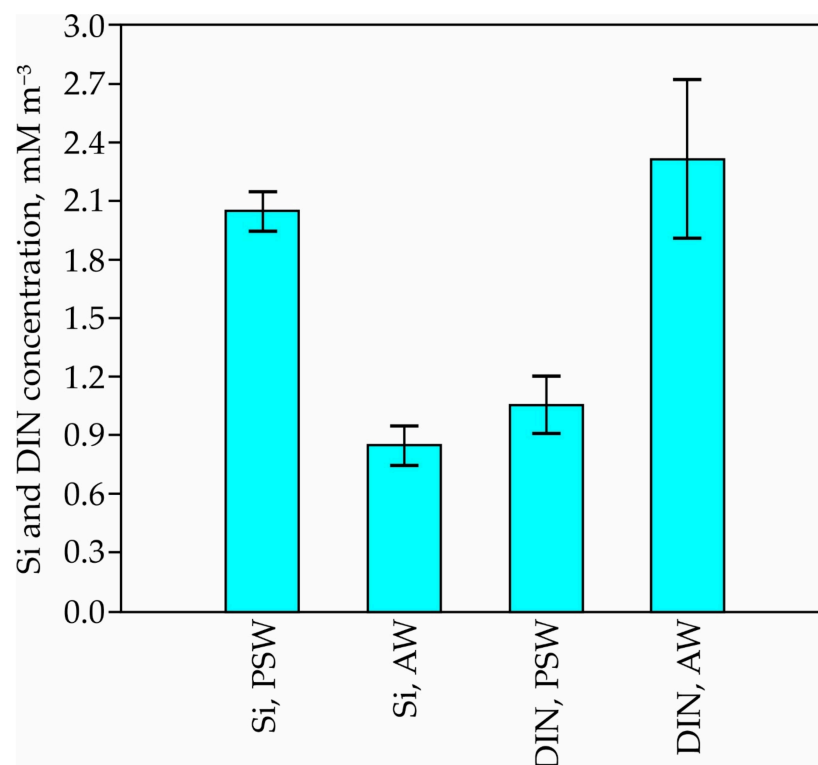


Figure 6. Average silicon and DIN concentrations in the euphotic layer in PSW and AW.

3.2.3. Transect 3

At stations 7066 and 7067, surface temperature and salinity decreased slightly, and a seasonal thermocline was observed at a depth of approximately 40 m (Table S2; Figures 4 and S1). Stations 7087–7088 were characterized by temperatures $> 0\text{ }^{\circ}\text{C}$ throughout the entire water column, with surface temperatures exceeding $6\text{ }^{\circ}\text{C}$. A thin layer ($\sim 5\text{ m}$) of colder ($< 3\text{ }^{\circ}\text{C}$) and fresher (< 34.0) water, corresponding to PSWw, was observed at the surface of Station 7089. At stations 7086 and 7085, the thickness of this layer increased to 20 m, while surface temperature and salinity decreased. At stations 7083 and 7084, water temperature from the surface to depths of 11.5 m (Station 7083) and 16 m (Station 7084) was $< 0\text{ }^{\circ}\text{C}$. At Station 7083, the PSW core was located substantially deeper than at Station 7084. The lowest salinity was recorded at the surface of Station 7083. The maximum salinity and density gradients occurred at depths of 14–21 m, whereas at stations 7088 and 7089, these gradients were observed below 30 m. At stations 7082 and 7081, the upper 20 m layer consisted of PSWw (surface temperature $> 4\text{ }^{\circ}\text{C}$), mAW occupied the 20–35 m depth range, and AW lay below.

3.2.4. Transect 4

At stations 7069 and 7070, the upper 20 m layer consisted of mAW, with the AW layer located below (Figures 5 and S1; Table S2). At the remaining stations of the transect, the water column was characterized by PSW with reduced salinity (< 34.0) and a core extending from 6 to 66 m in depth. Surface water temperature was $< 0\text{ }^{\circ}\text{C}$, except at stations 7071–7073 and 7077, where PSWw was observed. In the MIZ, a sharp halocline developed between mPSW and PSW at depths ranging from 7.8 to 19.4 m.

3.3. Nutrients

The mean silicate concentration in the euphotic zone of AW was less than $1\text{ }\mu\text{M}$, approximately half that in PSW (0.85 vs. $2.05\text{ }\mu\text{M}$, respectively; t -test, $p < 0.001$) (Figure 6). In contrast, the mean nitrogen concentration was significantly higher in AW (t -test, $p < 0.001$).

The silicate-to-nitrogen ratio (Si:N) proved to be a robust discriminator between AW and PSW, with mean values of 0.46 and 1.74, respectively (t -test, $p < 0.001$). Meltwater (mPSW) did not show significant differences from PSW in DIN concentrations (median values: 0.52 and 0.535 μM , respectively; $p > 0.05$).

3.4. Optical Properties of Water

The depth of the water layer where PAR is 1% of the surface value ranges from 27 to 60 m (Table S3), with an average of 40 m. The layer where PAR is 0.01% of the surface value is located at a depth of approximately 77 m. Comparison of the mean beam attenuation coefficient (BAC) in AW (0.43 m^{-1}) and PSW (0.27 m^{-1}) shows that this value is higher in AW, and the difference is significant (t -test, $p < 0.001$).

3.5. Phytoplankton

3.5.1. Ecological Complexes of Phytoplankton

To identify phytoplankton ecological complexes associated with each water mass, an initial checklist of species recorded during the study was compiled. To exclude incidental taxa from the overall species list, further analysis was restricted to species occurring in at least five samples (Table S6). Based on the obtained data matrix, phytoplankton groups were distinguished. The final list comprises 26 species from six taxonomic groups, which is a typical assemblage for the summer period in the high Arctic latitudes, where diatoms and dinoflagellates dominate. It includes 10 diatom species, 11 dinoflagellate species, 2 coccolithophore species, and one representative each of haptophytes, chrysophytes, and ciliates. This list was used for statistical validation of the characteristic phytoplankton composition in different water masses and for the identification of indicator species.

Multivariate analysis of phytoplankton communities, comprising diatoms, dinoflagellates, coccolithophores, haptophytes, and ciliates (Table S6), revealed that water mass type explains 28% of the total variation in community composition (PERMANOVA, $F = 14.68$, $p = 0.001$). This proportion of explained variance is substantially higher than that obtained from analyses based on diatoms alone ($R^2 = 0.21$), demonstrating the critical importance of including all taxonomic groups. Pairwise comparisons with Bonferroni correction confirmed significant differences between all pairs of water masses (Table 2). The magnitude of the t -statistic is proportional to the ecological distance between water masses, with t -values increasing alongside greater spatial separation along the latitudinal gradient.

Table 2. Pairwise comparisons among water masses (PERMANOVA).

Pairwise	t-Stat	p (Raw)	p (Bonferroni)
AW vs. mAW	2.85	0.001	0.003
AW vs. PSW	3.42	0.001	0.003
mAW vs. PSW	1.95	0.008	0.024

SIMPER (Similarity Percentages) analysis was employed to identify the species contributing most to the dissimilarity in phytoplankton composition among the three water masses (Table 3). The analysis was based on a presence/absence matrix combining diatoms and dinoflagellates. Taxa accounting for the top 50–58% of cumulative dissimilarity were considered as primary discriminators. For AW, the main contributors included species of the genus *Tripes*, the pennate diatom *Navicula planamembranacea*, and *Stephanopyxis turris*. For mAW, the heterotrophic dinoflagellates *Gyrodinium lachryma* and *Protoperidinium granii* were the key discriminators. For PSW, the characteristic species were the polar taxa *Protoperidinium islandicum*, *Rhizosolenia hebetata* f. *hebetata*, and *Porosira glacialis*. The highest dissimilarity was observed between AW and PSW, while the lowest

dissimilarity occurred between mAW and PSW; the AW–mAW pair exhibited an intermediate level of dissimilarity.

Table 3. Similarity Percentages (SIMPER) analysis. Species and their contributions to dissimilarity among water masses.

Species	Group	Contribution (%)	Cumulative (%)
AW vs. PSW—Average Dissimilarity: 0.76			
<i>Tripes spp.</i>	AW	15.80	15.80
<i>Navicula planamembranacea</i>	AW	13.50	29.30
<i>Protoperidinium islandicum</i>	PSW	11.20	40.50
<i>Stephanopyxis turris</i>	AW	9.80	50.30
<i>Rhizosolenia hebetata</i> f. <i>hebetata</i>	PSW	8.50	58.80
AW vs. mAW—Average Dissimilarity: 0.64			
<i>Tripes spp.</i>	AW	17.50	17.50
<i>Navicula planamembranacea</i>	AW	12.80	30.30
<i>Gyrodinium lachryma</i>	mAW	10.50	40.80
<i>Protoperidinium granii</i>	mAW	9.20	50.00
<i>Stephanopyxis turris</i>	AW	8.10	58.10
mAW vs. PSW—Average Dissimilarity: 0.58			
<i>Protoperidinium islandicum</i>	PSW	14.80	14.80
<i>Gyrodinium lachryma</i>	mAW	12.50	27.30
<i>Rhizosolenia hebetata</i> f. <i>hebetata</i>	PSW	10.20	37.50
<i>Protoperidinium granii</i>	mAW	9.50	47.00
<i>Porosira glacialis</i>	PSW	7.80	54.80

Indicator species analysis (IndVal) confirmed *Navicula planamembranacea*, *Tripes spp.*, *Stephanopyxis turris*, *Protoperidinium depressum*, and *Coccolithus pelagicus* (IndVal > 0.65, $p < 0.001$) as robust indicators of Atlantic Water (AW, Table 4). In contrast, *Rhizosolenia hebetata* f. *hebetata*, *Protoperidinium islandicum*, *Porosira glacialis*, and *Mesodinium rubrum* were identified as indicators of Polar Surface Water (PSW, IndVal > 0.62, $p < 0.001$). Interestingly, species such as *Gephyrocapsa huxleyi*, *Thalassiosira rotula*, *Phaeocystis pouchetii*, and *Monochrysis* sp. were not identified as exclusive indicators of modified Atlantic Water (mAW). This absence of unique indicator taxa reflects the transitional nature of mAW, which shares assemblage traits with both Atlantic and Arctic water masses.

Table 4. Indicator values (IndVal) of dominant phytoplankton species across water masses.

Species	Taxonomic Group	Water Mass	IndVal	p -Value	Indicator Status
<i>Rhizosolenia hebetata</i> f. <i>hebetata</i>	Diatoms	PSW	0.9	<0.001	Strong indicator of PSW
<i>Navicula planamembranacea</i>	Diatoms	AW	0.88	<0.001	Strong indicator of AW
<i>Tripes spp.</i>	Dinoflagellates	AW	0.82	<0.001	Strong indicator of AW
<i>Stephanopyxis turris</i>	Diatoms	AW	0.82	<0.001	Indicator of AW
<i>Porosira glacialis</i>	Diatoms	PSW	0.78	<0.001	Indicator of PSW
<i>Rhizosolenia styliiformis</i>	Diatoms	AW	0.75	<0.001	Indicator of AW
<i>Protoperidinium islandicum</i>	Dinoflagellates	PSW	0.71	<0.001	Indicator of PSW
<i>Protoperidinium depressum</i>	Dinoflagellates	AW	0.68	<0.001	Indicator of AW
<i>Coccolithus pelagicus</i>	Coccolithophores	AW	0.65	<0.01	Indicator of AW
<i>Mesodinium rubrum</i>	Ciliates	PSW	0.62	<0.01	Indicator of PSW
<i>Gephyrocapsa huxleyi</i>	Coccolithophores	AW/mAW	0.6	<0.05	Weak indicator of mAW
<i>Thalassiosira rotula</i>	Diatoms	mAW	0.6	<0.05	Indicator of mAW
<i>Phaeocystis pouchetii</i>	Haptophytes	mAW/PSW	0.55	<0.05	Weak indicator of mAW
<i>Monochrysis</i> sp.	Chrysophytes	mAW/PSW	0.5	<0.05	Weak indicator of mAW

3.5.2. Phytoplankton Composition and Biomass Along Transect 1

This transect was characterized by a relatively high abundance of coccolithophores, which decreased markedly at stations influenced by Polar Surface Waters (PSW; Stations 7052 and 7053) (Tables S5 and S7–S9). The contribution of diatoms to the phytoplankton community in Atlantic Waters (AW) was particularly significant in both branches of the West Spitsbergen Current (WSC). *Rhizosolenia styliformis* and *Stephanopyxis turris* dominated in the eastern branch, whereas *Navicula planamembranacea* prevailed in the western branch. Diatom biomass was higher in the western branch than in the eastern branch.

Total phytoplankton biomass in PSW was significantly higher than in AW (194.1 vs. 48.5 mg m⁻³, respectively; *t*-test, *p* = 0.008) (Table S8). This increase was driven by a greater contribution of dinoflagellates (*p* = 0.008) and chrysophytes (*p* = 0.038) compared with AW. At the northernmost stations (7052 and 7053), influenced by meltwater, the ice-associated diatom *Porosira glacialis* was detected. Additionally, the diatom assemblage included the pelagic cold-water species *Eucampia groenlandica* and *Rhizosolenia hebetata* f. *hebetata*.

Dinoflagellates of the genera *Tripes* and *Protoperidinium depressum* were characteristic of AW, whereas *P. islandicum*, *P. granii*, and *Gyrodinium lachryma* were most frequently encountered in PSW and modified Atlantic Waters (mAW).

Depth-integrated phytoplankton biomass in PSW was more than twice that in AW (5.2 vs. 2.3 g m⁻²; *t*-test, *p* = 0.01) (Table S7). This difference was attributed to elevated contributions of dinoflagellates, chrysophytes, and small flagellates (*t*-test: *p* = 0.02, 0.005, and 0.04, respectively).

3.5.3. Phytoplankton Composition and Biomass Along Transect 2

All stations along this transect were located within the AW domain. Phytoplankton abundance and biomass were low at all stations (Table S5). The vertical distribution of the biomass maximum differed between regions: on the shelf it was confined to the pycnocline separating cold, fresh surface waters from the underlying AW, whereas at offshore stations it occurred in the surface layer (Table S2).

The total phytoplankton biomass was consistently dominated by coccolithophores, chiefly *Coccolithus pelagicus* and, to a lesser extent, *Gephyrocapsa huxleyi* (Table S8). Heterotrophic dinoflagellates were also prominent, including the cold-water *Gyrodinium lachryma* and the warm-water *Protoperidinium depressum*, together with *Prorocentrum minimum*. Among diatoms, the warm-water Atlantic species *Navicula planamembranacea*, *Stephanopyxis turris*, and *Rhizosolenia styliformis* prevailed (Table S5).

3.5.4. Phytoplankton Composition and Biomass Along Transect 3

Based on hydrophysical characteristics, the eastern part of Transect 3 (Stations 7066–7089) was located within the AW domain. On the shelf and slope affected by the eastern branch of the WSC, the dominant phytoplankton complex comprised the warm-water Atlantic diatoms *Navicula planamembranacea*, *Rhizosolenia styliformis*, and *Stephanopyxis turris* (Tables S5, S6 and S9), accompanied by the large cold-water diatom *Rhizosolenia hebetata* f. *hebetata*. In the open waters (Stations 7087–7089), the dominant complex shifted to spring-bloom species, including the diatoms *Chaetoceros gelidus* and *Eucampia groenlandica* and the haptophyte *Phaeocystis pouchetii*. The number of spring-bloom species increased westward and peaked in the frontal zone on its Atlantic side (Station 7089) (Table S5).

Westward of Station 7084, surface water temperature dropped below zero and warm-water Atlantic species were no longer recorded in significant numbers. Cold-water species appeared instead, including the diatom *Porosira glacialis* and the chrysophyte *Monochrysis* sp.; in terms of biomass, however, the large dinoflagellate *Gyrodinium lachryma* dominated (Table S9). The cold-water dinoflagellate *Protoperidinium islandicum* was also recorded.

A two-layer structure was observed at Stations 7081 and 7082. In the upper PSW layer, the cold-water diatom *Rhizosolenia hebetata* f. *hebetata* and the dinoflagellates *Protoperidinium islandicum*, *P. granii*, and *Gyrodinium lachryma* were present, whereas AW occurred below 35 m. At the interface between these water masses, at a depth of 34 m, the AW-associated *Rhizosolenia styliformis* and the modified mAW-typical haptophyte *Phaeocystis pouchetii* exhibited intense growth (Table S9).

Depth-integrated biomass in Arctic-origin waters (PSW) exceeded that in AW by more than a factor of two (133.1 vs. 51.9 mg m⁻³; *t*-test, *p* = 0.04; Table S7). This difference was driven by the substantially greater biomass of dinoflagellates in PSW (62.9 vs. 15.3 mg m⁻³; *t*-test, *p* = 0.04).

3.5.5. Phytoplankton Composition and Biomass Along Transect 4

Dinoflagellates dominated the depth-integrated biomass, with the exception of Station 7078, where diatoms prevailed (Table S7). The highest total biomass was observed in surface waters over the shelf (Station 7069) and was comparable to that recorded at stations in the marginal ice zone (MIZ) (Stations 7081 and 7083, Transect 3). In the Atlantic Water Barents Current (AWBC), the maximum total biomass occurred at depths of 35–36 m, within the nutricline (Tables S4 and S8). These subsurface maxima consisted either of diatoms alone (Station 7070) or of diatoms and dinoflagellates in equal proportions (Station 7072), with diatoms of the genus *Thalassiosira* dominating at these stations.

The Atlantic diatom species indicative of the West Spitsbergen Current (WSC)—namely *Rhizosolenia styliformis* and *Navicula planamembranacea*—were recorded only over the shelf (Tables S5 and S6). In contrast, the cold-water diatom *Rhizosolenia hebetata* f. *hebetata* occurred throughout the upper 50 m layer at all stations along Transect 4, reaching maximum abundance at 9 m depth at Station 7078, in meltwater at −1.04 °C above the halocline (Tables S5, S6 and S9). The chrysophyte *Monochrysis* sp. was predominantly found in the AWBC and was absent from the PSW. Conversely, at Stations 7076–7079 within the PSW, the small ciliate *Mesodinium rubrum* occurred in high abundance and biomass in the upper 20 m layer.

3.6. Biomass as an Indicator of Water Masses

The depth-integrated total phytoplankton biomass in the euphotic zone differed significantly among AW, PSW, and mAW (Table 5). The highest biomass values were observed in PSW (one-way ANOVA, *p* < 0.05). However, only dinoflagellate biomass differed significantly among the water masses. Coccolithophores were significantly more dominant in AW than in PSW and mAW.

Table 5. Depth-integrated (weighted average) values of total phytoplankton biomass (mg m⁻³), diatoms, dinoflagellates, coccolithophores, and small flagellates in AW, PSW, and mAW.

Parameter	AW	PSW	mAW	<i>p</i>
Total biomass	36.3	85.5	58.6	<0.05
Diatoms	14.6	26.8	16.9	>0.05
Dinoflagellates	14.9	46.8	33.4	<0.05
Coccolithophores	2.7	0.2	8.5	<0.05
Small flagellates	4.1	3.1	3.3	>0.05

Based on the maximum biomass values at each station, the highest total phytoplankton biomass was observed at Station 7082, due to a diatom bloom (Table S9). Dinoflagellates dominated the biomass at most stations. The average maximum biomass values were higher in PSW (238.2 mg m⁻³) than in AW (80.0 mg m⁻³) and mAW (125.7 mg m⁻³).

Among the dinoflagellates, *Gyrodinium lachryma* was notable, occurring in high abundance in all water masses; however, this species reached its maximum biomass in mAW (Table S9). *Protoperidinium depressum* reached high biomass only in AW. *Gymnodinium* sp. was abundant in the western part of Transect 1, within the area influenced by PSW. The diatoms (*Rhizosolenia styliformis*, *R. hebetata* f. *hebetata*, and *Thalassiosira rotula*) and the haptophyte *Phaeocystis pouchetii* bloomed at the interface between PSW and AW. The ciliate *Mesodinium rubrum* was abundant in PSW.

4. Discussion

4.1. Ice Cover

The sea ice cover in the Eurasian sector of the Arctic Ocean exhibits high seasonal and interannual variability, which is regulated by wind intensity and direction, in addition to Atlantic Water (AW) inflows [77]. A comparison of sea ice conditions during the summers of 2020 and 2021 north of Svalbard revealed significant differences in ice edge position [78]. In August 2021, the ice edge was located considerably farther south than in August 2020.

4.2. Water Masses

In the Fram Strait, there are oppositely directed meridional flows of water masses of Arctic and Atlantic origin, which determine latitudinal gradients of hydrophysical parameters. In the eastern part, a powerful Atlantic Water (AW) current flows northward, and the transformation of this water mass occurs due to dilution by meltwater from Svalbard glaciers, resulting in lower temperature and salinity. Modified AW (mAW) is recorded north of the archipelago, where salinity ranges from 35.0 to 34.0 (Table S2). As AW moves northward, the salinity gradient increases, and a halocline forms, separating fresher surface waters from the more saline and denser AW. This vertical structure is typical of Arctic Ocean waters [56]. The sharp-gradient halocline enhances stratification, significantly reducing vertical exchange [8,9]. Nutrient supply decreases, leading to a decline in ecosystem productivity [79].

AW transports nutrients that determine the productivity of high-Arctic waters [12,80]. In the western part of the strait, Polar Surface Water (PSW) also undergoes transformation as it moves southward (Table S2); salinity and temperature increase due to mixing with the recirculating part of the AW flow [39–41]. The complex spatial structure of water masses and their significant horizontal and vertical transformation in the study area complicate their classification. Moreover, each region has its own specific characteristics. These factors preclude the construction of a universal water mass classification. We attempted to classify the water masses in our study area, taking into account the experience of researchers working in the Arctic region [57–59]. In the 0–500 m layer, we distinguish between AW and PSW using characteristic salinity and temperature boundaries (Table 1). Modified AW (mAW) is also identified, mainly north of Svalbard. Meltwater PSW (mPSW) is observed in the PSW, and warm PSW (PSWw) occurs in open water due to atmospheric forcing.

4.3. Nutrients

In Arctic waters, three main habitats exist: ice, sub-ice water, and open water. These habitats harbor different dominant phytoplankton assemblages. Moreover, phytoplankton composition within ice varies with ice age [81–83]. In spring, a phytoplankton bloom begins under the ice, and biomass can reach high values [19]. Under-ice phytoplankton growth is light-limited; therefore, the transition to open water is accompanied by an increase in primary production [16,37]. In open water, the limiting factor shifts from light to nutrients [35]. Nitrogen availability determines the productivity of pelagic Arctic ecosystems [84]. Our studies indicate that nitrogen concentration is a limiting nutrient

in Polar Surface Water (PSW). In Atlantic Water (AW), diatom growth is likely limited by silicon concentration, although nitrogen may also be limiting in some cases, and co-limitation by both nutrients can occur. We observed such a situation at Station 7066, where both silicon and nitrogen concentrations in the 0–22 m layer were low (Table S4). Nitrogen concentration in PSW varies seasonally: it is highest in winter and lowest in summer [78,85]. Periods of nutrient co-limitation may occur, leading to a corresponding restructuring of the community. Nevertheless, in PSW, nitrogen concentration remains the main regulator of phytoplankton taxonomic composition, as supported by several studies [86,87].

We assumed that phytoplankton growth is limited when nitrogen concentrations fall below 1 μM [38,88] and that diatom growth is limited by silicate concentrations below 1 μM [89–91]. Nitrate uptake rates may be limited at concentrations below 2 μM [92]. More precise threshold values vary among species, as they depend on minimum nutrient quotas, which in turn are a function of cell size [93,94].

According to Flores et al. [86], three nutrient regimes can be distinguished based on nitrogen and silicon concentrations. Our research indicates that at least two distinct regimes are present in our study area: one limited by silicon and the other by nitrogen. In PSW, relatively high silicon and low nitrogen concentrations were observed, with nitrogen limiting phytoplankton growth. In AW, silicon concentration was low, while nitrogen was relatively high. The Si:N ratio serves as a useful descriptor of these water masses, as confirmed by studies in the Labrador Sea [58].

Thus, the limiting factor changes along both meridional (northward) and latitudinal (east–west) gradients. A consequence of this shift in limiting factors is a restructuring of the phytoplankton community.

4.4. Phytoplankton Composition and Biomass

4.4.1. Ecological Complexes of Phytoplankton in the Fram Strait

The phytoplankton complexes identified in the Fram Strait are distinct species assemblages that characterize the main water masses of this region, which are delineated primarily by salinity (Table 1). PERMANOVA shows that these water masses (AW, mAW, and PSW) differ significantly in their phytoplankton community composition, and the differences remain statistically significant after the Bonferroni correction. Thus, water mass identity is the primary driver of phytoplankton community structure, which directly supports our hypothesis that distinct water masses are characterized by distinct dominant species.

SIMPER and IndVal analyses further confirm the fundamental distinction among AW, mAW, and PSW (Table 4). AW is characterized by a warm-water complex comprising dinoflagellates of the genus *Tripos* and *Protoperidinium depressum*, large diatoms (*Navicula planamembranacea*, *Rhizosolenia styliformis*, and *Stephanopyxis turris*), and the coccolithophore *Coccolithus pelagicus*; these species serve as reliable indicators of Atlantification (Figure 7). PSW is strictly associated with a cold-water complex consisting of the dinoflagellate *Protoperidinium islandicum*, the diatoms *Rhizosolenia hebetata* f. *hebetata* and *Porosira glacialis*, and the ciliate *Mesodinium rubrum*. The transitional state is represented by mAW, whose marker species include the diatom *Thalassiosira rotula*, the coccolithophore *Gephyrocapsa huxleyi*, the haptophyte *Phaeocystis pouchetii*, and the chrysophyte *Monochrysis* sp.

All identified species serve as bioindicators of their respective water masses. The large diatom *Porosira glacialis* is associated with first-year ice [65,95], so its presence in Polar Surface Water (PSW) is expected. *Rhizosolenia styliformis* was identified as an indicator of the West Spitsbergen Current (WSC) in the mid-20th century [46], and *Navicula planamembranacea* serves as an indicator of Atlantic Water (AW) [58]. Notably, Paasche [46] did not mention *N. planamembranacea* as an AW indicator in the North Atlantic, suggesting that

the appearance and mass development of this species at such high latitudes may be a consequence of climate change. Likewise, *Coccolithus pelagicus* is typical of North Atlantic waters [96], and the long-term northward shift in *Tripes* species has been documented as evidence of climate change [50].

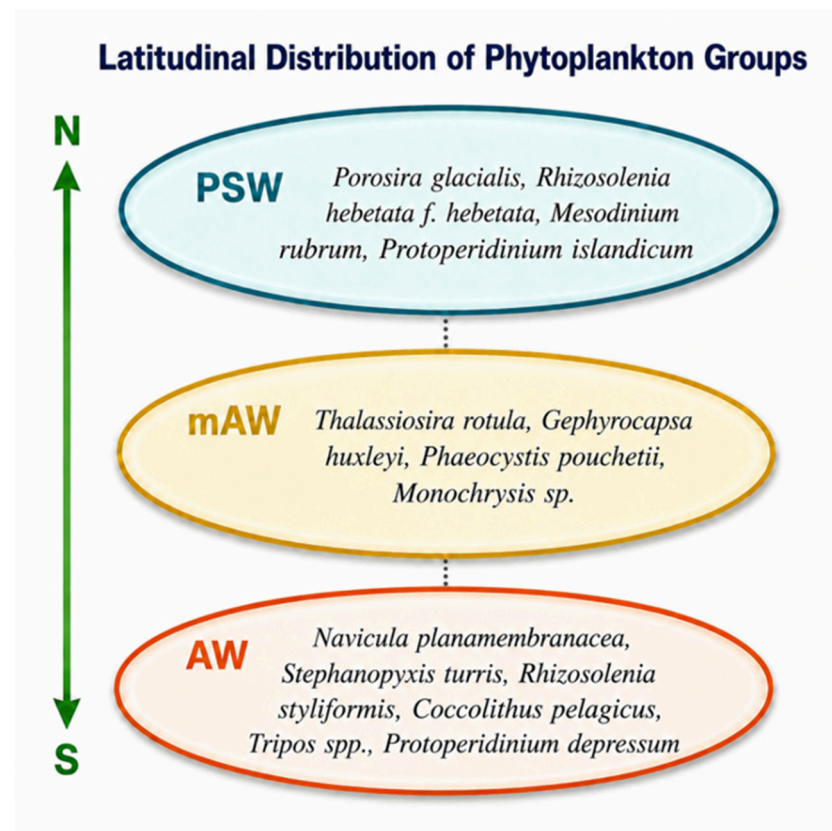


Figure 7. Phytoplankton indicator species associated with different water masses in the Fram Strait.

Thus, the transformation of Atlantic water masses during their northward progression—cooling and salinity changes—is accompanied by a substantial restructuring of the phytoplankton community. Our hypothesis that changes in the physicochemical properties of seawater drive the corresponding transformation of phytoplankton composition is statistically validated by our data.

However, some species proved to be unreliable markers of specific water masses. These include the cosmopolitan dinoflagellate *Prorocentrum minimum* [97]. Although *Gephyrocapsa huxleyi*, a cosmopolitan coccolithophore, occurred as a purely Atlantic species in previous studies, in our data it appeared primarily as a representative of modified Atlantic Water (mAW), which in the Fram Strait typically has temperatures of 3–5 °C. This range, however, may not be optimal for the growth of this alga: its maximum growth rate in monoculture lies well outside this interval [98]. Furthermore, species characteristics do not always coincide with those reported in the literature. For example, *Thalassiosira gravida* is considered by some authors a cold-water species [87], by others a polar species [99], and by still others an Arctic-temperate one [100]; in our study, however, it was not a reliable marker of PSW. Similarly, *T. rotula* is considered a temperate species by Giesler et al. [99], but our findings indicate that in the Fram Strait it is typical of mAW at temperatures of 3–5 °C.

Our grouping is not directly related to the three general biogeographic distribution types for diatoms—Arctic, Arctic-temperate, and cosmopolitan [101,102]. Rather, it allows us to predict the dominant phytoplankton composition from the thermohaline structure

and, in turn, to solve the inverse problem of predicting water mass structure from phytoplankton composition.

The applicability of dinoflagellates as bioindicators is species-specific. Some species, such as those of the genus *Triplos*, are confined to a single water mass within fairly narrow temperature ranges, whereas others occur across various water masses and wide temperature ranges. An example is *Gyrodinium lachryma*, whose high abundance was recorded in both warm AW and cold PSW (Table S9). We previously found a correlation between dinoflagellate and small flagellate biomass at high Arctic latitudes [103], and in summer many Arctic dinoflagellates possess photosynthetic pigments [104]. Large dinoflagellates are mixotrophs whose growth is sustained by both photosynthesis and phagotrophy [105,106]. The presence of an innate (constitutive) or acquired (non-constitutive) pigment apparatus [107], active swimming, and diverse feeding modes on small-celled phytoplankton [108–111] provide large dinoflagellates with additional advantages for survival under suboptimal conditions, making them widespread in the Arctic [112]. Mixoplankton thus play a crucial role in shaping high-latitude productivity.

Diatoms and dinoflagellates can grow rapidly at temperatures far from their optima [99,113,114]. Temperature changes during northward and westward movement elicit responses not only from the physiology of individual species but also from the entire ecosystem through complex biotic interactions [99,115,116]. Autotrophic and heterotrophic metabolic processes have different temperature sensitivities [117], and other environmental factors, such as irradiance and photoperiod, change simultaneously [33], modifying species-specific responses to temperature change [118]. Moreover, during the transition from AW to PSW, concentrations of the two main nutrients—silicon and nitrogen—change, leading to a shift in the limiting factor, which can also affect the response of phytoplankton to temperature [119–121]. Ultimately, predicting phytoplankton species composition in response to temperature change under natural conditions cannot be explained solely by temperature response curves obtained from monocultures.

4.4.2. Phytoplankton Composition Along the Transects

In the first half of August 2021, phytoplankton in the study area was predominantly in the late stages of succession, characterized by large diatoms and dinoflagellates [122].

On Transect 1, the presence of two distinct water masses—AW and PSW—determined differences in the composition of dominant species. The eastern part of the transect was characterized by elevated biomass of species typical of AW. Moving westward, the water masses underwent transformation, and the phytoplankton composition changed accordingly: AW representatives disappeared, while species characteristic of mAW (*Monochrysis* sp.) appeared. At stations closest to the Greenland shelf, within the PSW, the community included indicator species (*Porosira glacialis*, *Rhizosolenia hebetata* f. *hebetata*, *Protoperdinium islandicum*). Dinoflagellates *P. granii* and *Gyrodinium lachryma*, which are widely distributed in the North Atlantic and adjacent waters, were common along the transect [101,123,124].

On Transect 3, in the eastern part where the two branches of the WSC converge, AW indicator species (*Rhizosolenia styliformis*, *Navicula planamembranacea*) dominated. Westward, they were replaced by spring-bloom species (*Chaetoceros gelidus*, *Eucampia groenlandica*, *Phaeocystis pouchetii*) [24,124]; only one of these (*P. pouchetii*) is an indicator of mAW. The elevated species diversity is attributed to the complex water dynamics: AW and PSW meet and mix due to opposing currents, creating spatial environmental heterogeneity. An additional factor is active eddy formation—eddies of different polarities modulate vertical fluxes, generating diverse conditions for phytoplankton [39–41]. One mechanism that enhances local diversity and forms mixing zones is the intensive horizontal advection of Atlantic phytoplankton communities along eddy peripheries (the “suitcase hypothesis” [125]).

Thus, the high species diversity on Transect 3 reflects the formation of multiple ecological niches driven by complex dynamic processes.

In the MIZ area of Transect 3, a two-layer structure developed within the euphotic zone: PSW occupied the upper layer, underlain by AW (Stations 7082 and 7081). The PSW layer was characterized by a high abundance of the cold-water pelagic diatom *Rhizosolenia hebetata* f. *hebetata*. Owing to its large cell size, this species has higher silicon and lower nitrogen content per cell. At the PSW–AW interface, the more warm-water Atlantic species *Rhizosolenia styliformis*—whose cells are less silicified but contain more nitrogen—developed abundantly. It was *R. styliformis* that provided the maximum phytoplankton biomass, owing to the interaction between silicon-rich PSW and nitrogen-rich AW. This mechanism explains why the MIZ is considered the most productive area in the Fram Strait [126]. These stations exemplify how horizontal advection of AW not only alters environmental conditions but also transports Atlantic species that thrive under high-Arctic conditions [62,127]. The two-layer structure, with PSW representatives dominating the upper layer and AW indicator species in the lower layer, and the highly productive zone that developed at the PSW–AW interface—where the maximum biomass of the study period was recorded—both confirm our hypothesis on the formation of enhanced productivity zones within the euphotic zone at the boundary between polar surface and Atlantic waters.

Transect 4 is located north of Svalbard, in the Nansen Basin, where AW turns eastward, forming two flows of transformed Atlantic water—the Svalbard and Yermak branches. According to some studies, both branches merge into a single current in the Nansen Basin, yet the exact location of their confluence remains debated [12]. This area is characterized by strong interannual variability in hydrography, nutrient distribution, and chlorophyll-*a* concentration [80,128]. Sea ice conditions, particularly its thinning due to the increasing influence of AW, are also a significant factor affecting phytoplankton [129,130].

Our data indicate that the phytoplankton composition in the two branches differed substantially in the western Nansen Basin and on the adjacent northern Svalbard shelf. The community composition in the Svalbard branch generally corresponded to that of the Atlantic domain of the Fram Strait. In the AW flow along the shelf break (Stations 7070 and 7072), deep biomass maxima were composed mainly of dinoflagellates and diatoms of the genus *Thalassiosira*. AW indicator diatoms—*Rhizosolenia styliformis* and *Stephanopyxis turris*—were observed primarily in shelf and slope waters (Stations 7069 and 7070) at temperatures of 4.1–4.4 °C and salinities corresponding to mAW (34.02–34.05).

In the deep-water stations of the Yermak branch, from the Yermak Plateau eastward along the ice edge, the AW core was located at greater depth. Nevertheless, layers with salinities ≥ 34.0 remained within the euphotic zone, precluding nitrogen limitation of phytoplankton growth. The temperature of the upper productive layer (<0 °C) led to the dominance of cold-water PSW indicator species (*Rhizosolenia hebetata* f. *hebetata*, *Porosira glacialis*). The maximum abundance of *R. hebetata* f. *hebetata* at Stations 7078 and 7079 was associated with the halocline at 8–10 m depth, which separated the modified polar surface waters (mPSW) from the main PSW body. At other stations (e.g., Station 7076), a deeper halocline (down to 20 m) combined with cloud cover limited the abundance of this species due to insufficient irradiance. Calculations showed that at depths >20 m at Station 7076, the irradiance was about $2 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, which is close to the compensation point [131]. In the surface layer, another PSW indicator—the ciliate *Mesodinium rubrum*—developed instead. Thus, the position of the halocline regulates the occurrence of the PSW indicator species.

5. Conclusions

In the Fram Strait, Atlantic Waters (AW) flow northward through the eastern part of the strait, while Arctic waters move southward through the western part. During transit, these water masses undergo significant transformation of their physical and chemical characteristics, including salinity, temperature, density, and nutrient concentrations. Based on thermohaline structure, three types of water masses are distinguished: AW, modified Atlantic Waters (mAW), and Polar Surface Waters (PSW).

These three water masses differ notably in nutrient regime. AW have low silica concentrations, which limit diatom growth, and relatively high nitrogen concentrations. In contrast, PSW exhibit the opposite pattern: silica concentrations are relatively high, while phytoplankton growth is limited by nitrogen availability.

These differences in nutrient and physical properties manifest in a specific phytoplankton composition for each water mass, as confirmed by multivariate statistical analysis (PERMANOVA). Indicator species for each water mass were identified using SIMPER and IndVal methods.

Three phytoplankton complexes were distinguished: Arctic (cold-water), transitional, and Atlantic (warm-water). The cold-water indicator complex includes taxa characteristic of PSW: the diatoms *Porosira glacialis* and *Rhizosolenia hebetata* f. *hebetata*, the dinoflagellate *Protoperidinium islandicum*, and the ciliate *Mesodinium rubrum*. For mAW, characteristic species include the diatom *Thalassiosira rotula*, the coccolithophore *Gephyrocapsa huxleyi*, the haptophyte *Phaeocystis pouchetii*, and the chrysophyte *Monochrysis* sp. Warm AW are dominated by *Navicula planamembranacea*, *Stephanopyxis turris*, *Rhizosolenia styliiformis*, the dinoflagellates *Protoperidinium depressum* and *Tripes* spp., and the coccolithophore *Coccolithus pelagicus*.

Moving from south to north through the Fram Strait and from east to west toward the Greenland shelf, a sequential replacement of Atlantic species by transitional and subsequently by Arctic species is observed in the Marginal Ice Zone (MIZ). The composition and biomass of phytoplankton in the MIZ depend largely on the spatial position of AW. When PSW and AW are simultaneously present within the euphotic zone, a two-layer structure forms: the cold-water species *R. hebetata* f. *hebetata* dominates in the upper PSW layer, while the more warm-water Atlantic species *R. styliiformis* prevails at the interface between PSW and AW. The high abundance and biomass of large diatoms (*R. hebetata* f. *hebetata* and *R. styliiformis*) in the MIZ are associated with increased inflow of AW. The position of the halocline regulates the composition of dominant phytoplankton in PSW: when the halocline is shallow within the euphotic zone, *R. hebetata* f. *hebetata* dominates, whereas when the halocline is significantly deepened, the ciliate *M. rubrum* contributes the predominant biomass.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/environments13080464/s1>, Figure S1. T-S curves for all studied stations in 2021. Table S1. Station coordinates, date and time of sampling, and depth at the station. Table S2. Temperature, salinity, density, and CTD Chl a at the surface, depth of maximum temperature gradients, salinity, density, chlorophyll maxima, maximum and minimum temperatures, core depth of AW, and intersection with 0 °C. Table S3. The beam attenuation coefficient (BAC), surface water temperature, fluorescence readings, and depth of occurrence of 1% and 0.1% of the surface PAR. Table S4. Salinity, temperature, and concentrations of phosphorus, silicon, and nitrogen and their ratios at various depths of the studied stations in 2021. AW is highlighted in red, PSW in blue, and mAW in yellow. The limiting concentrations of silicon and nitrogen are highlighted in blue, and silicon concentrations from 1 to 2 µM in yellow. Table S5. The species composition of phytoplankton at all stations of Transects 1–4 in 2021. Diatoms (turquoise), coccolithophores (crimson), *Monochrysis* sp. (yellow), *Mesodinium rubrum* (red), and *Phaeocystis pouchetii* (green) are highlighted in color. Di-

noflagellates are not highlighted in color. Table S6. Phytoplankton species that occurred in more than five samples. Table S7. Weighted average biomass of all systematic and size groups and total biomass of phytoplankton. Table S8. The maximum values of the total phytoplankton biomass, as well as diatoms, dinoflagellates, coccolithophores, small flagellates, and chrysophytes and their contribution to the total phytoplankton biomass in the transects in 2021. The groups whose contribution to the total phytoplankton biomass exceeded 50% are highlighted in red. Table S9. Phytoplankton species with a biomass exceeding 100 mg m^{-3} . Diatoms (turquoise), *Mesodinium rubrum* (red), and *Phaeocystis pouchetii* (green) are highlighted in color. Dinoflagellates are not highlighted in color.

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