Seasonality in phytoplankton communities and production in three Arctic fjords across a climate gradient

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ABSTRACT

Phytoplankton communities and production in Arctic fjords undergo strong seasonal variations. Phytoplankton blooms are periods with high primary production, leading to elevated algal biomass fueling higher trophic levels. Blooms are typically driven bottom-up by light and nutrient availability but may also be top-down controlled by grazing. While phytoplankton spring blooms are common across all Arctic systems, summer and autumn blooms and their drivers are less predictable. Here we compare the long-term ($\geq$4 years) bloom phenology and protist community composition in three Arctic fjords: Nuup Kangerlua in western Greenland, Ramfjorden in northern Norway, and Adventfjorden in western Svalbard. While Nuup Kangerlua is impacted by tidewater glaciers, Ramfjorden and Adventfjorden are impacted by river-runoff. We discuss and contrast the presence and predictability of spring, summer, and autumn blooms in these fjords and the main physical, chemical, and biological drivers. Spring blooms occurred in all three fjords in April/May as soon as sufficient sunlight was available and typically terminated when nutrients were depleted. Chain-forming diatoms together with the haptophyte *Phaeocystis pouchetii* were key spring bloom taxa in all three fjords. Summer blooms were found in Nuup Kangerlua and Ramfjorden but were not common in Adventfjorden. In Nuup Kangerlua nutrient supply via subglacial upwelling was the key driver of a diatom-dominated summer bloom. This summer bloom extended far into autumn with strong winds resupplying nutrients to the surface later in the season. In Ramfjorden runoff from a vegetated catchment provided organic nutrients for a flagellate-dominated summer bloom in 2019. A late autumn bloom dominated by *Skeletonema spp*. and other chain-forming diatoms was present after nutrients were resupplied by wind mixing. In Adventfjorden, we observed only minor summer blooms in 2 of the 8 years, while autumn blooms were never observed. With global warming, we suggest that summer blooms will be negatively impacted in fjords where tidewater glaciers retreat and become land terminating. In fjords with rich vegetated catchments, harmful algal blooms may occur more frequently as summers and autumns become warmer and wetter. However, for fjords in high-Arctic latitudes (>78 N), the day length will continue to restrict the potential for autumn blooms.

1. Introduction

High latitude fjords, particularly those with tidewater glaciers are considered hotspots of marine primary productivity (Juul-Pedersen et al., 2015; Hopwood et al., 2020; Meire et al., 2017; Vonnahme et al., 2020). Primary production in these systems is predominantly driven by phytoplankton fueling a productive food web (Rysgaard and Nielsen, 2006; Stoecker and Capuzzo, 1990; Vargas et al., 2006). Major Arctic settlements, such as Nuuk, Tromsø, and Longyearbyen are relying on the diverse natural resources in these productive fjords for fishery, hunting, recreation, and tourism. In Nuup Kangerlua, for example, a high Greenland halibut catch has been associated with high local phytoplankton production throughout summer (Meire et al., 2017). Fjords are also hotspots for species relying on a cold local climate acting as a climate refuge from global warming (e.g. Arimitsu et al., 2008).

Phytoplankton production undergoes strong seasonal variations

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(Eilertsen and Taasen, 1984; Hegseth et al., 2019; Juul-Pedersen et al., 2015). At high latitudes, sunlight limits primary production during winter (Berge et al., 2015; Berge and Johnsen, 2020; Eilertsen and Taasen, 1984; Johnsen et al., 2020). As soon as sunlight increases in spring, phytoplankton spring blooms can start to form (Eilertsen and Taasen, 1984). Spring blooms are well described in boreal and sub-Arctic marine systems and are often considered the most productive season of the year (Eilertsen and Taasen, 1984; Hegseth et al., 2019). Growth rates are primarily driven by light and nutrients while loss rates are influenced by advection, sinking, grazing, viral lysis, and parasites (Collins et al., 2009, Hassett et al. 2016). The balance between growth and loss rates determines the intensity of the bloom. Earlier studies suggested that a shallow and stable mixed surface layer is necessary for phytoplankton to stay in the euphotic zone and produce high biomass in spring ("critical depth hypothesis"; Sverdrup, 1953). Later studies found that spring blooms can already start in fully mixed water columns and suggested that a positive net heat flux, limiting thermal convection, is sufficient to establish a spring bloom ("critical turbulence hypothesis"; Huisman et al., 1999). A fully mixed layer can also be beneficial for the establishment of the spring bloom, due to reduced grazing pressure ("Dilution-Recoupling hypothesis"; Behrenfeld and Boss, 2014; Behrenfeld, 2010). The different hypotheses may apply in different systems, or at different times (Vonnahme et al., 2022). Arctic spring bloom communities are rather consistent across studies and are typically dominated by chain-forming diatoms in early spring, often being replaced by the haptophyte *Phaeocystis pouchetii* when silicate becomes limiting (Hegseth et al., 2019; Krawczyk et al., 2018; Meshram et al., 2017).

While spring blooms are extensively studied in the Arctic, few studies focus on summer and autumn blooms (Eilertsen and Taasen, 1984; Juul-Pedersen et al., 2015; Vonnahme et al., 2022). Towards the end of the spring bloom, nutrients are depleted, and grazing pressure may increase, leading to a low production and biomass. This low productive season is often dominated by potentially mixotrophic flagellates (Assmy et al., 2023; Eilertsen and Taasen, 1984). Phytoplankton blooms in summer (Arrigo et al., 2017; Juul-Pedersen et al., 2015) and autumn (Vonnahme et al., 2022) are often associated with resupply of new nutrients fueling mostly diatom blooms. Summer blooms in fjords with tidewater glaciers can be fed by nutrients from subglacial upwelling (e.g., Juul-Pedersen et al., 2015). Terrestrial inputs through river run-off can also be a key source of nutrients to Arctic ecosystems during summer (Terhaar et al., 2021). Autumn blooms are often associated with a weak stratification and increased wind mixing replenishing the summer depleted nutrients in the euphotic zone (Ardyna et al., 2014; Pogojeva et al., 2022). With climate change the Arctic summer and autumn blooms may increase in frequency and magnitude, as indicated by recent remote sensing-based studies (e.g., Zhao et al., 2022). Seasonal time series spanning several years in systems along climate gradients are needed to understand and assess the role of drivers affecting phytoplankton production and diversity in the present and future climate. Drivers may include bottom-up factors such as light availability, nutrient supply by upwelling, wind mixing or terrestrial inputs and top-down factors such as grazing pressure. All these drivers are variable over seasons and years.

To examine the effect of different environmental drivers on the bloom phenology in the different fjord systems, we compare three high-resolution multi-year time series (>4 years) from contrasting Arctic fjords. A previously unpublished 8-year time series from Adventfjorden (Isfjorden, Svalbard at 78°N) as a high latitude fjord system with relatively small tidewater glaciers. Two previously published time series of 3 and 1.5 years from the 1970s (Eilertsen and Taasen, 1984) and 2018/2019 (Coguiec et al., 2021; Vonnahme et al., 2022) in Ramfjorden, an intermediate latitude fjord system, lacking tidewater glaciers located at 69°N in northern Norway. A previously published time series from a West Greenland fjord system (Nuup Kangerlua at 64°N; Juul-Pedersen et al., 2015; Krawczyk et al., 2015) from 7 to 15 years as a lower latitude system with large tidewater glaciers. The fjords differ in their size,

depth, circulation patterns, light regimes, and in terms of the presence and size of tidewater glaciers, advection of warm and saline Atlantic influenced water inflow, sea ice cover, air temperatures, and precipitation.

The objectives of this study were to compare these three different fjords bloom phenology in terms of their distinct environmental and biological characteristics during spring, summer, and autumn blooms annually and interannually. Comparing these diverse fjords enables us to discuss the importance of different drivers and if they are universal for Arctic fjords, or unique to specific fjord systems. We hypothesize that sunlight as the key driver of spring blooms is universal across the Arctic, while drivers causing the presence or absence of summer and autumn blooms (e.g., subglacial upwelling, river runoff) may be very different depending on the fjord characteristics and geographical location.

2. Materials and methods

2.1. Study area

Sampling was conducted at Nuup Kangerlua time series station (NK, Greenland) as part of the Greenland Ecosystem Monitoring (GEM) programme (Fig. 1, Table 1), in Ramfjorden (RAM, northern Norway, Fig. 1), and at the Isfjorden Adventfjorden (IsA, Svalbard, Fig. 1) time series station. All fjord systems are important for local communities, fishery and hunting, and tourism. Nuup Kangerlua is located in West Greenland and the fjord has a comparable size to Isfjorden (Table 1; (Mortensen et al., 2018)). Ramfjorden is a northern Norwegian fjord within the Balsfjorden system (Table 1; Noji et al., 1993). The IsA time series station is located at the mouth of Adventfjorden, within the Isfjorden fjord system, which is the largest fjord of western Svalbard (Skogseth et al., 2020). Deep tidewater glaciers are present in Nuup Kangerlua (grounding line depth ca 250 m, Motyka et al., 2017) while no glaciers are present in the Ramfjorden (RAM) and the Balsfjorden system.Shallower tidewater glaciers are present (grounding line depths < 100 m; (Luckman et al., 2015)) in Isfjorden, but not in Adventfjorden (IsA). Terrestrial runoff from vegetated catchments is an important freshwater source for RAM and IsA, but less so for NK, which is further away from river inflow. All fjords have annual inflow of Atlantic-type water masses, albeit at different depths, different magnitudes, and with different Atlantic-type water properties (Mortensen et al., 2014, 2018; Skogseth et al., 2020). Atlantic-type water inflow in Ramfjorden and Isfjorden is shallower and characterized by a higher temperature and salinity than in Nuup Kangerlua. In Nuup Kangerlua Atlantic type water and coastal water inflow is limited by a sill of about 170 m depth (Mortensen et al., 2011). Balsfjorden is separated from the coastal water by a sill of 10–35 m depth (Oug and Høisæter, 2000), while, Isfjorden has no sills isolating Adventfjorden from the shelf break.

2.2. Atlantic type water inflow

The warm North Atlantic Current (NAC) is a major source of warm Atlantic type water into the western Norwegian fjords, including Ramfjorden (Fig. 1). An extension of this NAC into the high Arctic, known as the West Spitsbergen Current (WSC) impacts western Svalbard fjords to varying degrees with regular and rather massive influxes recorded into Isfjorden since 2005 (Skogseth et al., 2020). A colder, fresher Arctic water mass originating from the Eastern Spitsbergen current (ESC) also reaches the western Svalbard fjords isolating the fjords to some degree from Atlantic water inflow and causing the formation of Transformed Atlantic water (Skogseth et al., 2020). In Ramfjorden and Isfjorden several local water masses are also formed by influences from local runoff, wind mixing, surface radiation, and sea ice formation and melt. The western part of Greenland has a weaker influence from Atlantic type water compared to Svalbard. The Atlantic water from the Irminger current is separated from the coast by a cold East Greenland Current, which gradually mixes with the Atlantic water,
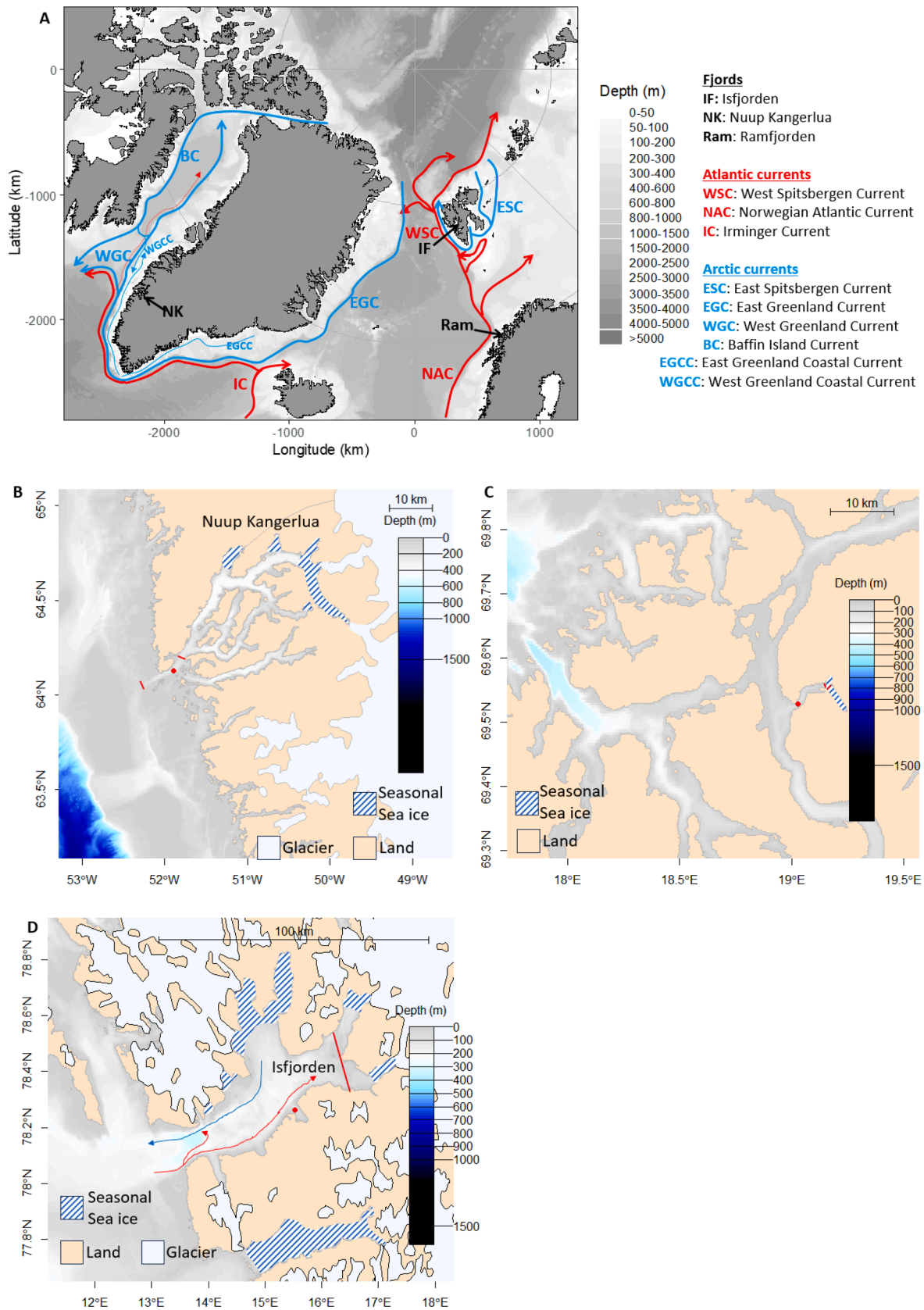
Fig. 1. Sampling locations. A) Overview showing the location of the studied fjord systems and the flow of major ocean currents into the fjord systems in study (UTM projection). B-D) Location of the three studied fjord systems in B) Nuup Kangerlua (NK), C) Ramfjorden (RAM), and D) Adventfjorden (IsA) showing the location of the time series stations, seasonal sea ice cover, depth and inflow and outflow of Atlantic influenced currents in Isfjorden (arrows), and locations of relevant sills (red line).

Table 1
Characteristics of the three sampling stations.

	NK	RAM	IsA
Fjord	Nuup Kangerlua	Ramfjorden	Isfjorden
Latitude	64° 07′ N	69° 31′N	78° 15′N
Longitude	51° 53′ W	19° 02′E	15° 32′E
Area	2013 km^2	13 km^2	3084 km^2
Max depth	625 m	130 m	120 m
Tidal range	4–5 m	ca 2 m[7]	0–2 m[6]
Daylight (Apr-Oct)	8–21 h	6–24 h	0–24 h
Sampling period	2005–2019	1976–1978[2] 2018–2019 [3,4]	2012–2014 2015–2019 (only physical)
Tidewater glacier	Deep (250 m)	None	Shallow (<100 m)
River runoff	Yes	Yes	Yes
Sill depth	170 *m*	10–35 *m*	None

([1] (Mortensen et al., 2014); [2] (Eilertsen & Taasen, 1984); [3] (Coguiec et al., 2021); [4] (Vonnahme et al., 2022); [5] (Skogseth et al., 2020); [6] (Zając-kowski & Włodarska-Kowalczuk, 2007); [7] RAM Tidal range: Kartverket. https://www.kartverket.no/til-sjos/se-havniva/resultat?id=139281&location=Ramfjorden).

which then becomes the West Greenland Current flowing and at times entering the fjords in West Greenland alongside coastal water masses. The Atlantic-type and Atlantic derived water in West Greenland is deeper and more diluted with local and coastal water masses than in Norway and Svalbard.

2.3. Sampling

At NK samples were taken following the guidelines of the Greenland Ecosystem Monitoring (GEM) programme (https://www.g-e-m.dk). RAM samples were taken as described by (Eilertsen and Taasen, 1984) in the 1970 s and as described by (Vonnahme et al., 2022) and (Coguiec et al., 2021) in 2018/2019. The samples at IsA were taken following guidelines described by (Marquardt et al., 2016), and as described on the University Centre in Svalbards website (UNIS, 2021). Sampling procedures are given in brief below.

Conductivity, Temperature, and Density (CTD) Profiles of temperature, salinity, density, and chlorophyll-a fluorescence were measured via CTD profiles in all fjords, except for 1976 in RAM when temperature was measured using Nansen bottles with reversing thermometers and salinity was measured manually using a Beckmann Salinometer (Eilertsen and Taasen, 1984). At IsA a SAIV SD204 or SD208 CTD probe (SAIV A/S, Bergen, Norway) equipped with a chlorophyll-a fluorescence sensor (Seapoint, USA) was used. At NK, a Seabird SBE19 + CTD equipped with a biospherical QSP-2300L PAR sensor, Seapoint Chl-a fluorometer and a Seapoint turbidity sensor was used. In Ramfjorden 2018/19, a Seabird SBE19 + CTD with chlorophyll-a fluorescence and PAR sensor and at times a CastAway CTD was used (Vonnahme et al., 2022). In 2019, an additional chlorophyll-a fluorescence sensor was deployed on a mooring at 18 m depth (Coguiec et al., 2021). In 1977 and 1978 CTD profiles in Ramfjorden were taken with a Mark III CTD probe (Eilertsen and Taasen, 1984). Surface irradiance (PAR) data were compiled from the Adventdalen weather station (KandZ PQS1 sensor, Kipp and Zonen Inc, Delft, The Netherland model CNR1) on Svalbard, the ClimateBasis-Nuuk weather station in Greenland (part of GEM; g-e-m.dk), and the UiT weather station Lufft WS50, model 2770 for the solar radiation sensor located in Tromsø, Norway.

2.4. Water sampling

Water samples at all stations were collected using Niskin bottles. At NK samples were taken from 0, 1, 5, 10, 15, 20, 30, 40, 50, 100, 150, 250, and 300 m, at RAM samples were taken from 0, 1, 2, 4, 8, 16, 32,

and 50 m in the 1970 s (Eilertsen and Taasen 1984) and from 5, 30, and 125 m in 2018/2019 (Vonnahme et al., 2022) and at IsA samples were taken from 5 m, 15 or 25 m, and 60 or 75 m. The water samples were analyzed for nutrients (Silicate, Nitrate + Nitrite, Phosphate) and Chlorophyll-a concentrations, and ^{14}C-DIC based incubations for primary production estimates based on light response curves (RAM and IsA).

2.5. Nutrients

Nutrients were measured from pre-filtered samples in Greenland (GF/F filter), and Norway (0.2 µm syringe filter), while samples at IsA were not filtered. All samples were stored at -20 °C before measurements. Photometric nutrient measurements were done using standard colorimetric methods (Andreae, 2018) on a spectrophotometer (Shimadzu, UVmini-1240, NK), or nutrient analyzers (Flow Solution IV analyser (OI Analytical USA) Tromsø, QuAAtro 39, IsA and RAM (2018/19) (Dąbrowska et al., 2021; Kubiszyn et al., 2017; Marquardt et al., 2016).

2.6. Chlorophyll-a

Chlorophyll-a (Chl-a) samples were filtered onto GF/F glass microfiber filters and extracted in 96 % Ethanol (NK and RAM) or in 100 % Methanol at IsA for approx. 24 h (at room temperature at NK, at 4 °C at IsA and at RAM) and measured on a fluorometer (Turner TD-700 from 2005 to 2018 and Turner Trilogy from 2019 to 2020 at NK, Turner 10AUE at IsA and RAM). The samples were also acid corrected with 5 % HCl (at IsA and RAM), 200 µl 1 M HCl (at NK). Total Chl-a values were calculated as described in Sumanta et al., (2014).

2.7. Primary production

Primary production (NPP) was estimated after ^{14}C-DIC incubations in all fjords. At NK, NPP measurements were based on *in situ* ^{14}C-DIC incubations at 5, 10, 20, 30 and 40 m. The *in situ* DIC uptake was then corrected using the proportion of the light during the incubation time of the average daily light measured by the nearest weather station in Nuuk as described by Juul-Pedersen et al., (2015). At RAM, NPP was measured in the 1970 s via *in situ* incubation for 4–6 h with no light corrections as described by Eilertsen and Taasen, (1984).

At IsA primary production was only measured in 2022 and the data have not been published previously. At IsA primary production was estimated via ^{14}C –DIC uptake at different light intensities. Water samples from 5 m and 20 m depth were transferred into 73 mL cultivation flasks and 175 µl ^{14}C –bicarbonate (20 µCi ml^{-1}) was added before incubation for 2 h at *in situ* temperature using a cooling bath water circulating through the experimental set-up. 3 flasks were incubated in the dark and 11 flasks were incubated at decreasing light intensities between ~ 1200 and 40 µE µE m^{-2} s^{-1} (measured within the bottles using a Li-cor PAR sensor). After the incubation, samples were filtered onto 25 mm GF/F filters and acidified (100 µl 1 M HCl) in 20 mL liquid scintillation vials for at least 12 h (lid closed) before drying for another 12–24 h (lid open). The ^{14}C uptake was measured after adding Ultima Gold™ Scintillation cocktail and measurement on a liquid scintillation counter. Light response curves using Chlorophyll-a specific (based on Chlorophyll measurements) primary production rates were then calculated using the phytotools package in R (Revell, 2024). Based on the Light response curve parameters, chlorophyll profiles based on chlorophyll-a profiles, PAR profiles, and daily PAR measurements, daily primary production was calculated.

2.8. Phytoplankton blooms

Bloom seasons were identified as an increase in Chl-a or NPP. A bloom between April and May is considered a spring bloom, a bloom

between July and August a summer bloom, and a bloom between September and October an autumn bloom.

Phytoplankton blooms and communities may vary substantially within a few weeks. Thus, monthly time series may, by chance, catch or miss the peak bloom periods in different years. Using community composition averaged over several years like at NK, allows us to identify the typical seasonal patterns, but does not represent interannual variability. At IsA a weekly to bi-weekly time series improved the temporal resolution in 2012–2013, but also implies that the 2014 monthly dataset may be different. In Ramfjorden, a bi-weekly sampling during the spring bloom allowed the spring bloom dynamics to be captured in more detail, but summer and autumn bloom communities may be affected by this bias.

2.9. Microscopy

Protist communities at NK and RAM were analyzed using light microscopic counts of water samples (Norway) and phytoplankton nets (10 μm mesh size in Norway from 30-0 m; 20 μm mesh size in Greenland from 60 to 0 m; (Krawczyk et al., 2015, 2018). All phytoplankton net samples were fixed in neutral Lugol solution (2 % fin. conc.). Protist communities at IsA were based on light microscopy (2011–14) of water samples fixed in acidic Lugol and borax-buffered formalin (2012–2014) as described by (Kubiszyn et al., 2017). All protist taxa were identified to the highest identifiable taxonomic level. While all phytoplankton datasets were obtained via light microscopy, some differences between the datasets may be due to methodological differences and limitations. NK samples are based on vertical phytoplankton net hauls, which may miss or under-represent smaller (<20 μm) species. Earlier comparisons between microscopy of water samples from discrete depths and phytoplankton nets showed a higher diversity in net samples, likely due to high vertical variability in the water column, which may lead to an underestimation of diversity at IsA (Vonnahme et al., in prep). The smaller phytoplankton net mesh size in Ramfjorden (<10 μm) and the unfiltered water samples at IsA might have caught smaller species. However, the key taxa discussed in this study (Diatoms and *Phaeocystis pouchetii*) are phytoplankton taxa that can be detected with all sampling methods, since their cell or colony size is > 20 μm. Microscopy datasets may be subject to a counter bias, e.g., different persons may identify individuals to different taxonomic levels. This counter bias is potentially a significant problem for rare or difficult to identify taxa (e.g., small flagellates, pennate single cell diatoms). The current study discusses the dominant phytoplankton taxa mostly on genus level during different blooms, which we consider less affected by a potential counter bias.

2.10. Zooplankton abundances

Count data for zooplankton grazers was adapted from studies by Balazy et al., (2021) and Stübner et al., (2016) or retrieved from Coguiec et al., (2021). Mesozooplankton abundances were estimated from zooplankton net hauls with a WP2 net (mesh size: 45 μm at NK, 64 μm at IsA and RAM) from 100 m to surface at NK and from close to the bottom to the surface at IsA (80–120 m) and RAM (115 m). The counts of each net haul are used to quantify mesozooplankton grazer abundances. While these data are comparable within each site and can show seasonal changes, caution must be exercised when attempting cross-site comparisons due to variations in sampling methods. While the different mesh sizes do not allow direct comparisons of total abundances between NK and IsA and RAM, the seasonality of zooplankton abundances within each site is used to discuss potential grazing pressure.

2.11. Statistical analysis

All measurements were averaged monthly across all years throughout the datasets, and seasonal cycles for nutrients (average at 0–15 m), surface PAR, Chl-a biomass, NPP and zooplankton grazers were analyzed. This regular data collection interval, spanning from bi-weekly to monthly observations, aggregated over several years, provided a robust basis for investigating seasonality over a complete annual cycle. Chl-a and NPP are also shown for all years, to discuss interannual variability. The stratification index was calculated based on sea water density data within the euphotic zone using the *stratif* function of the castR package as density differences between the shallowest (0–1 m) and 40 m (Jean-Olivier, 2021).

The *taxa.pooler* function (Gobet, 2010) was used to pool taxa at different taxonomic levels and the *Plot.Abund* function from the pastecs package (Grosjean and Ibanez, 2024) in R was used to calculate the five most abundant taxa (genera) in every sample for IsA. In this study, we conducted multivariate statistics on community structures for each station, each month and each year. We applied an NMDS to normalized phytoplankton abundances to study community dissimilarity and an RDA to study community variation under the constraint of environmental variables. *Decostand* from the package *vegan* was used to Hellinger transform the community data before an RDA, and the bray curtis distance was calculated using the *metaMDS* function for the NMDS. The RDA was calculated using the *rda* function, using the above transformed data (Legendre and Gallagher, 2001). Environmental data were standardized before they were used in RDA to constrain the community data. PAR, stratification index, nitrate and silicate concentration as main environmental variables affecting phytoplankton growth patterns were used to study changes in communities over the stations and years.

3. Results

Due to the latitudinal differences (64°N at NK, 69°N at RAM, 78°N at IsA,) the seasonal cycle of solar radiation differs between the fjord systems. IsA has a true polar night from the end of October to mid-February, while RAM has a shorter polar night from the end of November to the end of January. NK is below the polar circle and does not have a true polar night. While PAR levels at NK are low ($21.03\ \mu E\ m^{-2}\ s^{-1}$) between November and February, they are above the minimum required PAR level for phytoplankton to maintain photosynthesis of $0.5\ \mu E\ m^{-2}\ s^{-1}$ according to Kvernvik et al., (2018). In all fjords, surface PAR levels above $200\ \mu E\ m^{-2}\ s^{-1}$ (i.e., PAR threshold for net autotrophy; Hodal et al., 2012) are reached in March. In September, the surface PAR levels at NK decrease below $146\ \mu E\ m^{-2}\ s^{-1}$ reaching $43.3\ \mu E\ m^{-2}\ s^{-1}$ in October, while at RAM PAR levels decrease from 151 to $22\ \mu E\ m^{-2}\ s^{-1}$ and at IsA from 85 to $7\ \mu E\ m^{-2}\ s^{-1}$ in the same months.

3.1. Hydrography

All fjords show a strong seasonality in their hydrography with a generally more stratified water column in summer (July to October, Fig. 2). Surface temperatures in NK start increasing in May, whereas surface salinity starts decreasing in July and reaches its minimum of 28 in August. At the same time, temperature is increasing up to average temperatures of 6 °C. However, these values present monthly averages from 16 years, and temperatures can reach up to 8 °C and Salinity down to 19 in some years (Fig. S8). RAM has less data available and is more variable over the year and has the highest temperatures of all fjords (up to 12 °C in July), and a lower salinity of 25. Like NK, RAM surface temperatures start increasing in May. In contrast to NK and IsA, RAM has decreased surface salinities and a potentially stratified surface layer throughout the year, including winter freshwater lenses at the surface. At IsA temperature starts increasing in May and salinity starts decreasing in June, reaching a minimum of 32 in July, while the surface temperature increases to about 7 °C. In general IsA is the fjord with the highest salinities (up to 35). At IsA an increase in temperature and salinity, indicating Atlantic water, are present at relatively shallow depth (<60 m).
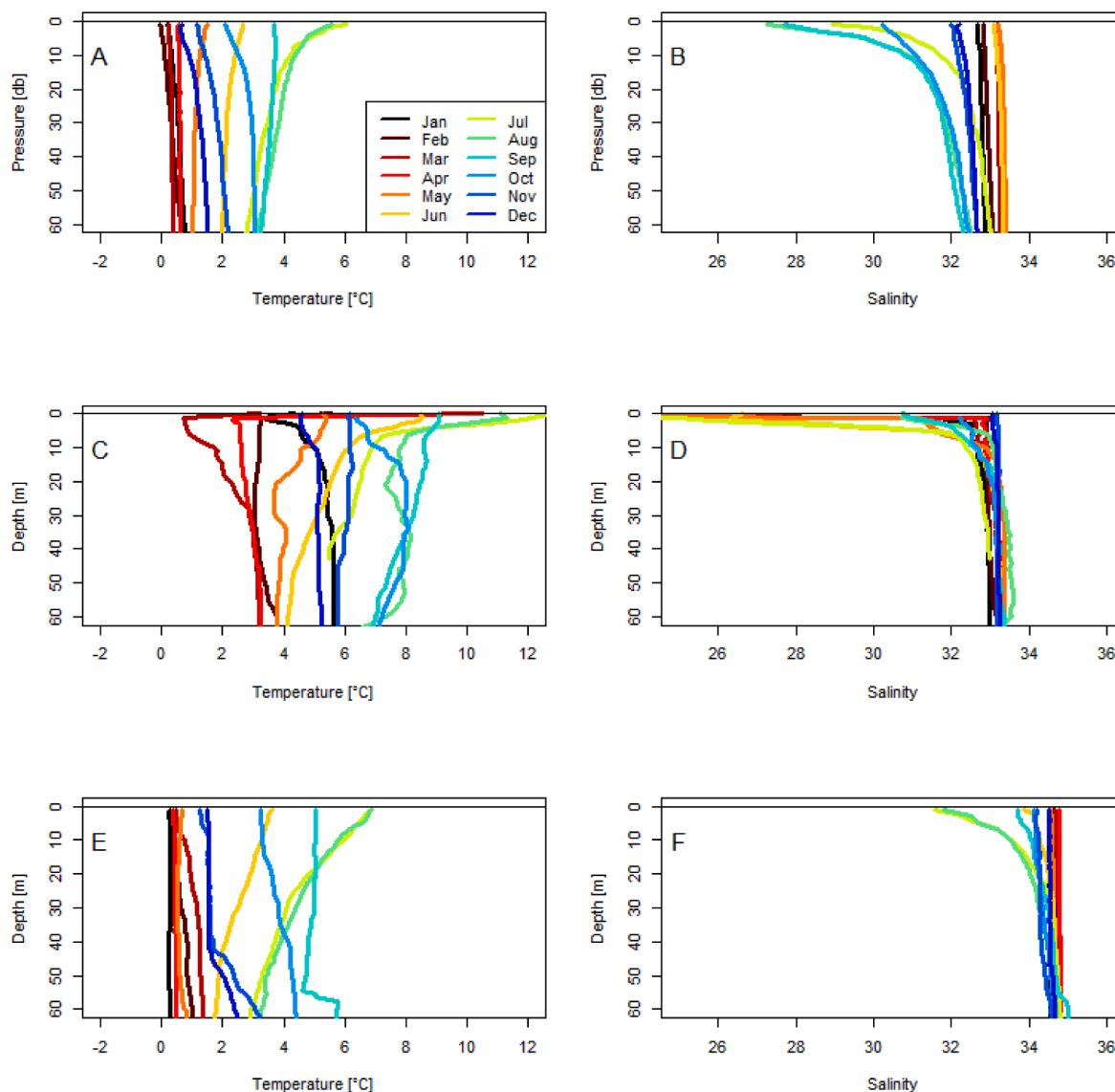
Fig. 2. Temperature (A,C,D) and Salinity (B,D,F) profiles in NK (A,B), Ram (C,D), and IsA (E,F). IsA and NK represent monthly averages, and Ram represent the year 2019.

3.2. Seasonality of algal biomass and primary production

All three fjord systems exhibited a pronounced spring bloom with a peak in both Chl-a concentrations and net primary production (NPP; Figs. 3 and 4). In NK and RAM, the spring bloom reached its peak (according to both NPP and Chl-a) in mid-April and early May, while the peak spring bloom (in Chl-a) at IsA showed interannual variability between the end of April (2013, 2015) and mid-June (2014, 2018, 2019). Maximum mean Chl-a concentration during the bloom were higher at NK (3.4 mg m^{-3}) than at IsA (1.1 mg m^{-3}) considering all measurements during the entire time series. However, Chl-a at IsA was consistently higher from 2012 to 2016 than between 2017 and 2019, indicating interannual differences. Following the spring bloom, Chl-a and NPP dropped rapidly until June in all fjords. In NK, a secondary summer bloom as elevated NPP and sometimes Chl-a was found in all years between July and August. At RAM, a summer bloom as elevated NPP was found during September 1976 and a summer and autumn bloom as elevated Chl-a during July and October 2019, in some years. At IsA elevated summer Chl-a was only measured in 2017 and 2019. During the NK summer peak, NPP typically increased, while Chl-a at times stayed relatively low compared to the NPP peak. At times of a large difference

between NPP and Chl-a, grazer abundances tend to be higher as well (Fig. S10). At IsA and NK, Chl-a and NPP dropped to a minimum from October until the end of the year, while distinct autumn blooms (high Chl-a and NPP) were present in RAM around the same time. At NK during some years, the summer blooms continued until September, masking a potential separate autumn bloom.

At IsA and NK, mesozooplankton grazer abundances (Fig. 4) showed overall different patterns than phytoplankton biomass (Chl-a) with low numbers during the spring bloom and a peak in July (Fig. 4). At IsA, zooplankton abundances started to increase in April, while at NK a similar increase was not seen before June. In RAM, grazer abundance patterns were very different with the highest abundances in October during the autumn bloom with only slightly elevated abundances during the spring and summer blooms but still a magnitude lower in abundance compared to IsA and NK.

The overall seasonality of nitrate and nitrite (NOx; Fig. 4) concentrations in the surface (0–15 m) was also comparable in the different fjords with maximum concentrations in winter (average: 5 μM at RAM, 7 μM at IsA, 8 μM at NK) before a steep decline in April with the onset of the spring bloom. The maximum bottom water nitrate concentrations were in a similar range to the surface concentrations (average: 5 μM at
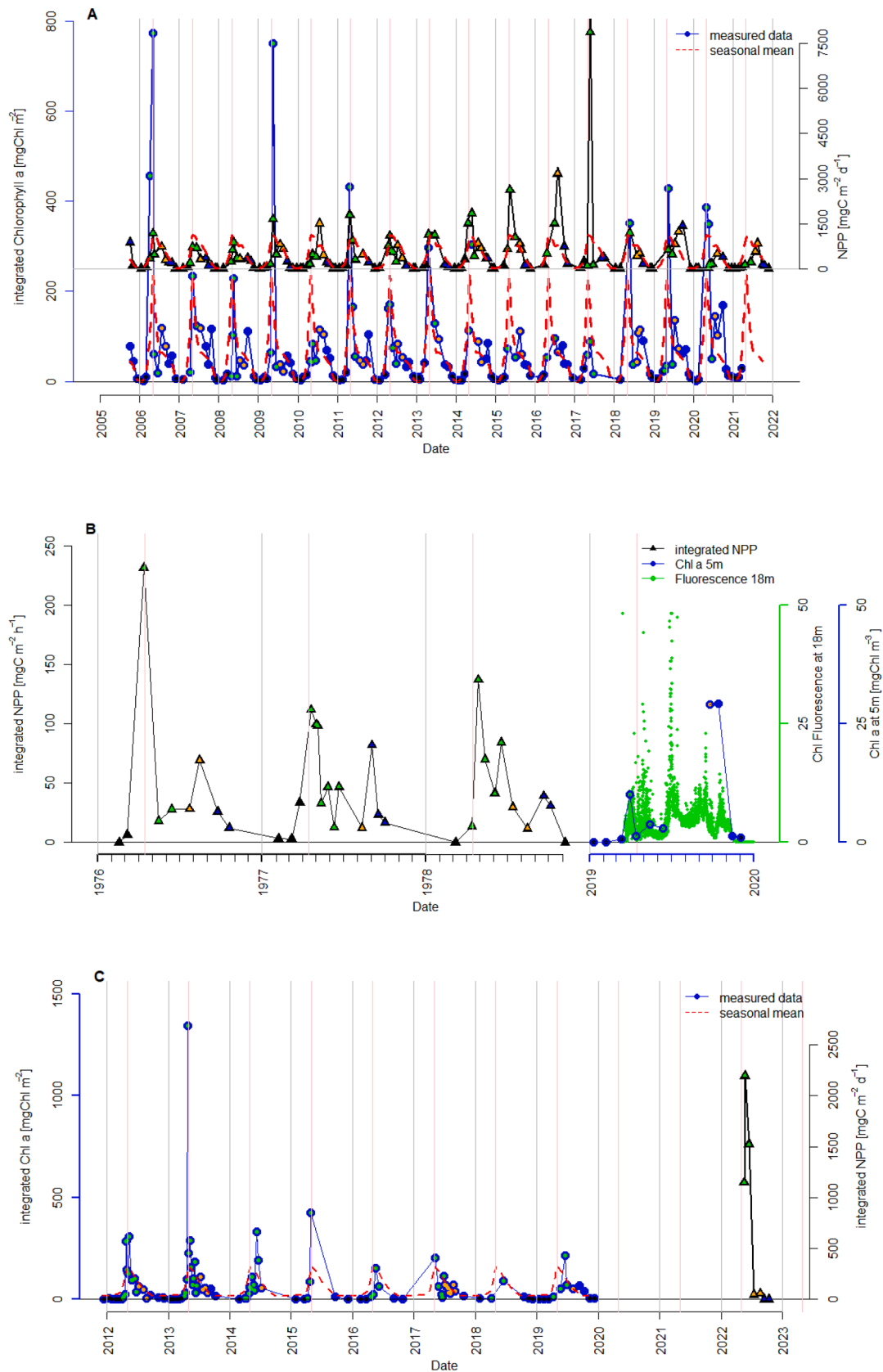
Fig. 3. Chlorophyll-a standing stocks (blue), chlorophyll fluorescence (green) based on mooring at 18 m depth in Ramfjorden (RAM), and net primary production (black) in A) Nuup Kangerlua (NK), B) Ramfjorden (RAM) and C) Isfjorden (IsA). Gray vertical lines indicate the beginning of each year, red vertical lines show the position of the spring bloom in April (Isfjorden) and May (Nuup Kangerlua, Ramfjorden). Red dotted lines in A) and B) show the monthly mean for all years. The inner colors indicate the season: black: winter, green: spring, orange: summer, and blue: autumn.
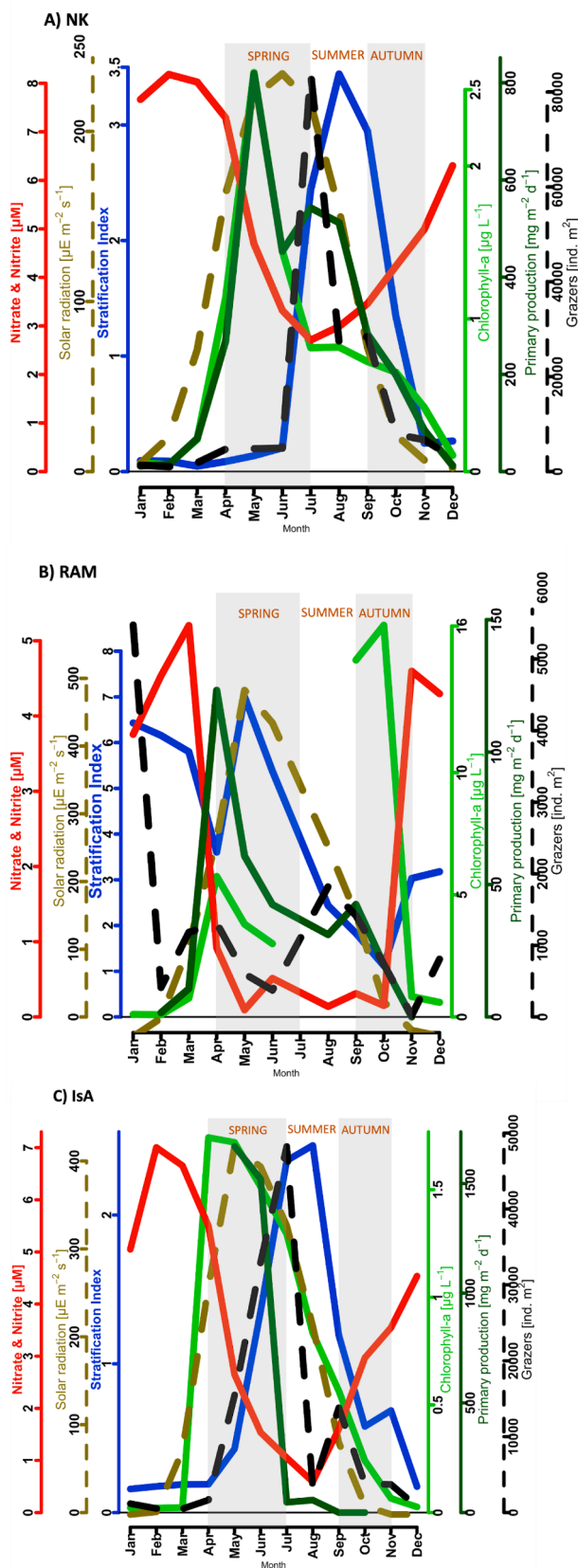
Fig. 4. Average seasonality of plankton (Average Chl-a biomass (0–15 m), mesozooplankton abundance) and primary production (NPP) and their drivers (average nutrients (0–15 m), light (0 m), stratification index) in A) Nuup Kangerlua (NK), B) Ramfjorden (RAM) and C) Adventfjorden (IsA). Note differences in scales.

RAM and IsA, 7 μM at NK). At NK, the lowest NOx concentrations of about 3 μM were reached in June/July, followed by an increase that coincided with the secondary summer bloom. At IsA NOx concentrations dropped to about 0.5 μM in August, a month later than at NK. In RAM, NOx was typically low throughout summer from May to October but may occasionally be resupplied via terrestrial runoff (Coguiec et al., 2021) and have been shown to increase from < 0.5 μM in late summer to 4.5 μM (Fig. 4B) in autumn compared to 3.5 μM at IsA (Fig. 4C) and 5 μM at NK (Fig. 4A) around the same time.

At NK, the increase of NOx and a secondary summer bloom also coincided with an increasing stratification index. The stratification index is primarily driven by sea surface salinity (0–5 m, linear regression $R^2 = 0.98$), with changes mainly due to glacial and snowmelt-based freshwater discharge and ice melt. Maximum stratification is reached in September, before a steep decline due to reduced freshwater discharge and increased autumn wind mixing. At IsA the stratification index starts to increase in April, further continuing to show a major rise in May and starts to decline in August and does not coincide with increased NOx in August. In RAM, the stratification index already increases in May/June after sea ice and snow melt and stays relatively high over summer reaching a maximum in July due to the combined effect of seasonal warming and river inflow. Winter melt events have been observed to increase winter stratification in 2019 (Stratification index: 6.1—6.6 in January-February).

3.3. Seasonality of protist communities

All fjord systems showed high diversity with seasonally distinct communities throughout the year (Dąbrowska et al., 2021; Krawczyk et al., 2015, 2018; Kubiszyn et al., 2017; Vonnahme et al., 2022). While spring bloom community compositions were overall comparable, summer and autumn communities differed taxonomically between the fjords (Fig. 5).

The spring bloom communities in all three fjords were dominated by the haptophyte *Phaeocystis pouchetii* and the diatom genera *Chaetoceros*, *Thalassiosira,* and sometimes *Fragilariopsis* (at IsA). However, community compositions at the beginning and end of the spring blooms varied between the fjords and years in the same fjord. The beginning of the spring bloom in Ramfjorden has been dominated by *Chaetoceros gelidus* (formerly *C. socialis:* Chamnansinp et al., 2013) in the 1970 s and 2019 (Eilertsen et al., 1981), typically being replaced by *P. pouchetii* towards the end of the bloom after silicate depletion. In Nuup Kangerlua, spring bloom taxa were more variable with various *Chaetoceros* and *Thalassiosira* species dominating in different years in combination with *P. pouchetii*. Only in 2009, *P. pouchetii* was absent (Krawczyk et al., 2015). In Isfjorden, where microscopy data are only available from late 2011 to 2014, spring bloom communities were very different in 2012 and 2013. In 2012, *P. pouchetii* was already dominant from the beginning with a smaller contribution from *Chaetoceros socialis* (Fig. 5C). In 2013 and 2014, the spring bloom communities were dominated by *Chaetoceros* spp. and *Thalassiosira* spp. with very low abundances of *P. pouchetii* (Dąbrowska et al., 2021).

The summer bloom communities at NK consisted of a few very abundant species such as *Chaetoceros* spp. and other chain forming centric and pennate (*Pseudo-nitzschia* spp.) diatoms. Also, *Phaeocystis pouchetii* was abundant in some years. While the moderate summer blooms in RAM during the 1970 s were also dominated by chain-forming centric diatoms and *Phaeocystis*, the strong summer bloom in 2019 was dominated by the potentially harmful chrysophyte *Chrysochromulina leadbeateri* (Eikrem and Throndsen, 1998; Karlsen et al., 2019; John et al., 2022). At IsA, summer blooms were only detected in 2017 and 2019, where no phytoplankton community data are available. During the low biomass summer conditions at IsA the plankton communities were more diverse and included diatoms, *Phaeocystis*, and unidentified flagellates. With the progressing summer season at IsA an increase in abundance of pennate diatoms like *Pseudo-nitzschia* was apparent during
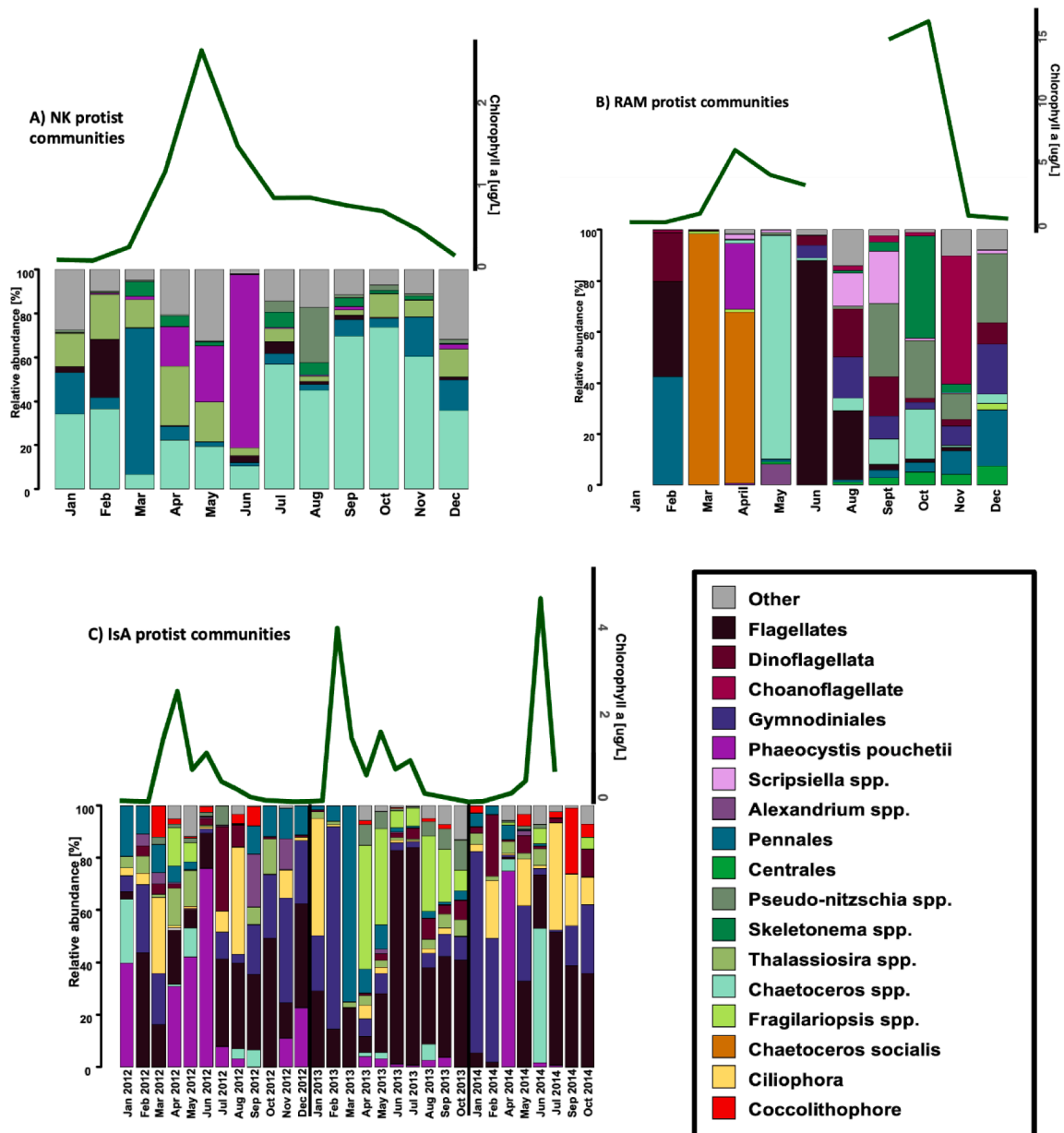
Fig. 5. Communities from A) Nuup Kangerlua (NK) between 2005–2019, B) Ramfjorden (RAM) between 2018–2019 and C) Isfjorden (IsA) between 2012–2014, showing all three years of data instead of monthly averaged throughout the dataset to highlight interannual differences between spring bloom communities.

July-August with a gradual reduction in abundance until the end of the year.

A discrete autumn bloom was only observed at RAM, with a continuous summer-autumn bloom at NK and no such bloom occurring at IsA. At RAM the autumn bloom was typically dominated by chain-forming diatom species that differed from those present during the spring bloom. *Skeletonema spp.* was abundant in 2018 and 2019, followed by *Pseudo-nitzschia spp.* Following the autumn bloom, different dinoflagellates and flagellates became dominant.

Non-bloom communities are very variable between fjords and years. At NK, diatoms were abundant throughout the year, while dinoflagellates, choanoflagellates, and other flagellates were abundant at RAM. Similarly, the IsA communities outside the blooms were dominated by dinoflagellates, and other flagellates, but also by ciliates.

3.4. Relation of phytoplankton seasonal changes to environmental variables

The NMDS shows the importance of seasonality for phytoplankton community composition at all fjords and time points (Fig. 6). Summer and autumn seasons differed greatly from spring at all fjords but especially at NK. Within the fjords, spring season communities were overall similar over the years,. Summer and autumn communities together formed two groups, one with NK, and the other with RAM and IsA combined. In the RDA, samples from NK have a wider spread. The seasonal grouping shown in the NMDS remains, now showing the environmental factors associated with this seasonal variation. Seasonal factors like PAR (Anova by terms: 3 %, p-value = 0.001) shaping the spring season community, and stratification index (2.5 %, p-value = 0.001) shaping the summer/autumn community. Samples from IsA and RAM form a group with lower seasonal variation, which may be due to the relatively limited number of years available for both fjords. Different
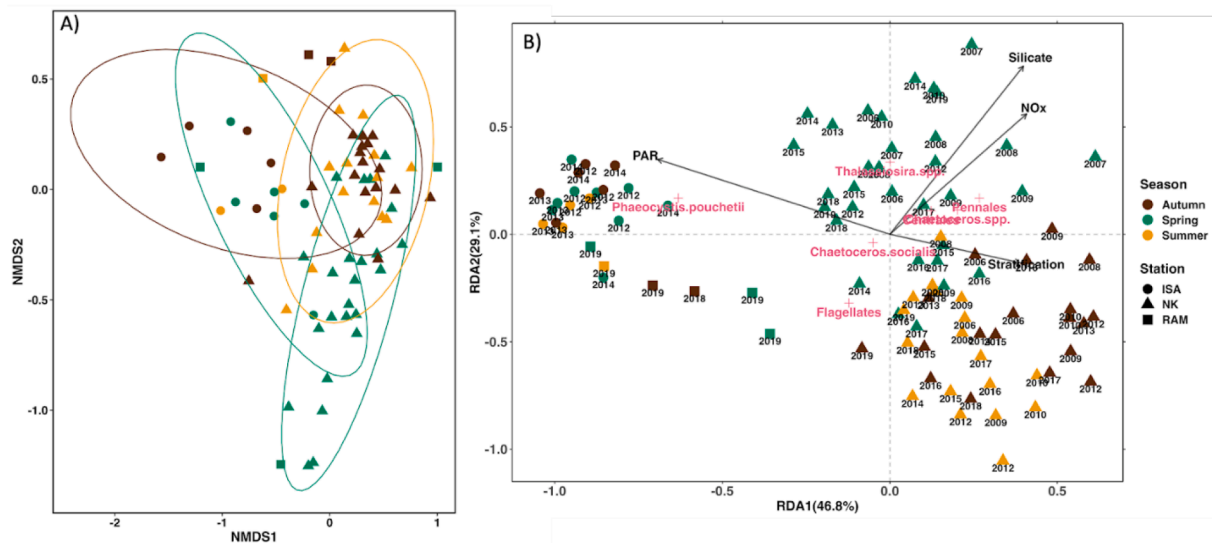
Fig. 6. NMDS (Stress: 0.191) where ellipses the signify at 95% confidence interval the distribution of the data in each group (A) and RDA (B) for all stations and seasons, where green represents spring bloom (April, May, June), yellow represents summer bloom/summer season (July, August) and brown represents autumn bloom/autumn season (September, October).

species show varying degrees of association with environmental gradients, with some being more generalist (e.g *Chaetoceros socialis and Thalassiosira* spp.) and others more specific to certain fjords and seasons (eg. *Phaeocystis pouchetii* in spring at NK). The distinguishing factor between summer and autumn communities at RAM plus IsA versus NK were flagellates being found more commonly at RAM and IsA and Centrales plus Pennales more commonly present at NK.

4. Discussion

The growing season of Arctic phytoplankton is generally constrained by light availability. When sufficient light is available, three potential blooms have been described: i) a spring bloom between April and June found in most high latitude fjords and open ocean systems, fueled by nutrients from winter mixing (Hegseth et al., 2019; Juul-Pedersen et al., 2015; Townsend et al., 1994; Vonnahme et al., 2022; Waniek, 2003), ii) a secondary summer bloom between July and August, likely triggered by subglacial upwelling (Juul-Pedersen et al., 2015; Meire et al., 2017) or episodic vertical mixing events (Iverson et al., 1974), and iii) an autumn bloom between September and October in fjords and oceans where autumn mixing due to strong winds and weakened stratification occurs before light becomes limiting (Ardyna et al., 2014; Vonnahme et al., 2022). Generally, nutrients are the key limiting factor during the growing period, but grazing pressure may additionally suppress biomass, especially in strongly stratified systems (Behrenfeld, 2010). The following sections discuss each of these seasons in detail using a comparative approach between the three fjord systems.

(i) Spring bloom.

A characteristic spring bloom was present in all three fjords. Light is the key limiting driver for the initiation of the spring bloom (Eilertsen et al., 1989), which is also evident from the three fjord systems where irradiance (PAR) had the strongest influence. Available light in the water column may be limited by the incoming solar radiation, sea ice, sediments, and deep vertical mixing (Sverdrup, 1953). There was no layer of freshwater, otherwise known as the freshwater lens, during the start of the spring bloom, in any of the fjords which contradicts the critical depth hypothesis (Sverdrup, 1953). Similar observations have been made in other Arctic fjords, such as Kongsfjorden on Svalbard (Hegseth et al., 2019; Assmy et al., 2023; Koenig et al., 2024), and

Balsfjorden, Porsangerfjorden, and Altafjorden in northern Norway (Eilertsen et al., 1981; Eilertsen and Taasen, 1984; Eilertsen and Frantzen, 2007). In Nuup Kangerlua, it has been suggested that a major part of the phytoplankton biomass may originate from the inner fjord, where stratification may be stronger due to local ice- and snow (Juul-Pedersen et al., 2015). However, at IsA, which is in direct proximity to a potential freshwater source, no freshwater lens was found during the initiation of the spring bloom. In Ramfjorden, it has been suggested that the critical turbulence hypothesis (Huisman et al., 1999) applies, after which a bloom can already start if the net heat flux at the surface-air interface reverses, which was the case in the presented data (Supplementary table 1; Eilertsen and Taasen, 1984; Vonnahme et al., 2022). Overall, the critical turbulence hypothesis appears to apply to all three fjords. If solar radiation were the sole driver of the spring bloom initiation, we would anticipate earlier blooms at lower latitudes such as NK, which we did not observe. Instead, we find a relatively late spring bloom at the low-latitude NK (April/May) compared to the earlier spring bloom at the mid-latitude RAM (April). In contrast to Ramfjorden and Isfjorden, the station NK is strongly affected by diapycnal tidal mixing, likely destabilizing the water column also in the absence of thermal convection (Mortensen et al., 2022). Consequently, a reversed heat flux, i.e., heating of the ocean by the atmosphere, may not be enough to produce a sufficiently stable surface layer in areas with strong tidal mixing. Thus, our study supports that in NK, phytoplankton biomass (Chl-a) may to a large degree be advected from the inner part of the fjord where tidal mixing is weaker, as suggested by Juul-Pedersen et al. (2015).

The typical spring bloom in all three fjords was characterized by various chain-forming diatoms (*Chaetoceros* spp., *Thalassiosira* spp.) and haptophytes (*Phaeocystis pouchetii*). These taxa are also common in spring blooms in other Arctic fjords, such as the Svalbard fjords Kongsfjorden and Hornsund and other North Atlantic fjords (Degerlund and Eilertsen, 2010; Smoła et al., 2017). The dominant diatom species appear to be variable between years and fjords. Some species may be associated with the advection of inoculum from nearby sea ice (e.g. *Fragilariopsis* spp. at IsA) or different water masses (AW vs polar water masses; Johnsen et al., 2018). Other species may be resupplied by winter storms from local resting spores in the sediment, which may explain the recurring dominance of *Chaetoceros socialis* in Ramfjorden. In Ramfjorden terrestrial runoff has also a strong impact on the fjord hydrography, as shown by winter melt events leading to low surface salinities which may increase the importance of local low-salinity adapted species

(Persson, 2020; Vonnahme et al., 2022). The spring bloom species *Phaeocystis pouchetii*, typically followed the diatom bloom, when silicate concentrations depleted. However, *P. pouchetii* may be absent or rare in some years, such as in 2009 at NK, and in 2014 at IsA (e.g., Krawczyk et al., 2015). The absence of *P. pouchetii* has generally been associated with interannual changes in Atlantic water inflow, upwelling, and nutrient dynamics (Krawczyk et al., 2015, Hegseth and Tverberg, 2013, Kubiszyn et al., 2017), showing the importance of multi-year time series to identify key drivers.

While nutrients are not limited in the beginning of the spring bloom, they may define the length of the bloom. Considering that NOx concentrations in the Atlantic core water are typically around 10 to 12 μM (Randelhoff et al., 2020), surface spring nutrient concentrations of 5 to 8 μM are relatively low, indicating incomplete winter mixing, or nutrient-poor Arctic or local water masses. In all fjords, bottom water NOx concentrations are comparable, showing that incomplete vertical mixing was not an issue. Instead, we suggest that nutrient-poor water masses, such as Arctic water masses (e.g. Baffin Bay Polar Water in NK), or local water masses (e.g. winter meltwater in RAM), are the main reason for the lower spring NOx concentrations. In RAM and IsA the termination of the spring bloom as a decrease in phytoplankton biomass and production was associated with a decrease of NOx below 1 μM. In contrast, NK NOx concentrations stay relatively high (3 μM), presumably due to supply by subglacial upwelling, leading into a summer bloom (Juul-Pedersen et al., 2015).

Grazing pressure may also drive the drop in total primary production and Chl-a biomass (Arendt et al., 2010; Juul-Pedersen et al., 2015). While spring mesozooplankton grazer abundances were low in Nuup Kangerlua, a higher abundance of smaller grazers or a higher proportion of larger or more efficient grazers in the mesozooplankton community, may still lead to a high grazing pressure (Arendt et al., 2010; Assmy et al., 2023; Tang et al., 2011). Earlier studies in NK suggest that top-down regulation by protozooplankton and copepods were negligible, only being responsible for grazing on 3 and 10 % of the primary production respectively during the post spring bloom conditions in late-May (Arendt et al., 2010; Tang et al., 2011). In comparison 44 % of the primary production was grazed by micro- and mesozooplankton in the Beaufort and Chukchi Seas in summer (Campbell et al., 2009), which was considered low due to an exported production of more than half of the primary production to the sea floor. The termination of spring blooms in Ramfjorden can be attributed to a depletion of nutrients within the euphotic zone and not the grazer abundances which are still below 1000 ind m^{-2} just after peak spring bloom (Fig. 3). Also, the strong stratification prevalent during this period restricts the vertical transport of nutrients from below the mixed layer depth, preventing their replenishment in the euphotic zone and contributing to the end of the bloom. Only in Isfjorden, grazer abundances increased around the same time as Chl-a and primary production decreased (Fig. 3), indicating that grazing may be locally important in terminating the spring bloom.

Climate change may lead to an earlier onset of a reversal of the thermal heat flux for the spring bloom. The earlier warming may lead to an earlier termination of thermal winter convection and thereby an earlier onset of the spring bloom. While an earlier bloom is possible in NK, the polar night at RAM and IsA sets constraints on the timing of the bloom start. However, increased Atlantic water inflow may increase the available bottom nutrients, which are currently lower than the winter Atlantic core water (Randelhoff et al., 2020). While grazer abundances are currently low during the spring bloom, an increased stratification may lead to increased grazing pressure in the surface layer due to weaker dilution effects (Behrenfeld, 2010).

(ii) Summer bloom.

In summer, nutrients are typically the key limitation for primary production. Thus, a resupply of nutrients to the euphotic depth is a prerequisite for summer blooms. A summer bloom has been described in fjords with tidewater glaciers, leading to the hypothesis that subglacial upwelling is key for resupplying nutrients to the euphotic zone (Juul-Pedersen et al., 2015; Meire et al., 2023). In Nuup Kangerlua, this mechanism is visible as a substantial increase in primary production, coinciding with an increase in the stratification index and decrease in surface salinity. A salinity decrease indicates an increase in glacial runoff, as discussed by Meire et al., (2017, 2023). In the Ameralik fjord, a fjord system neighboring Nuup Kangerlua without tidewater glaciers, no summer blooms have been detected so far, attributed to the lack of tidewater glaciers (Meire et al., 2023). Meire et al., (2023) argue that turbid surface meltwater inflow from the land-terminating glacier in Ameralik is limiting light and nutrients and thereby summer production in the fjord.

The tidewater glaciers in Isfjorden are downstream of the IsA station considering the fjord circulation and have therefore a negligible impact on the monitoring station. Yet, a minor summer bloom has been observed in 2017 and 2019. We suggest that nutrient inflow with river water may fuel summer blooms in some years. In fact, (McGovern et al., 2020) found high summer nutrient concentrations of 12 ± 7 μM NOx in the Adventelva river adjacent to the Isfjorden monitoring station, exceeding the highest concentrations found in the fjord, which may potentially fuel summer production. In addition, organic nitrogen with high concentrations in early summer (June, McGovern et al., 2020) may be available for primary producers after bacterial remineralization (Terhaar et al., 2021). While reducing PAR for phytoplankton, a high sediment load could also reduce the visibility for predators, which may reduce grazing pressure. (Bluhm & Gradinger, 2008). However, the summer bloom was very weak and not always present, indicating that the freshwater flux is either too low, or that the associated sediments are limiting production by light inhibition.

Further contradicting the notion that subglacial upwelling is vital for summer blooms in Arctic fjords, are observations in Kongsfjorden, a Svalbard fjord influenced by a tidewater glacier, where distinct summer blooms are not always present (e.g., Hegseth et al., 2019). Nutrient-poor local water masses or limited subglacial upwelling due to a shallow grounding line may explain the lack of summer blooms in some years (Hopwood et al., 2020). However, Halbach et al., (2019), estimated that 20 % of the summer NPP were fueled by subglacial upwelling of nutrients leading to a summer bloom in Kongsfjorden in 2017. Considering the close proximity of the sampling site (0.7 to 3.3 km) to the glacier terminus we suggest that the distance of the sampling station from the glacier is another important factor influencing localized summer blooms (Hopwood et al., 2020). A summer diatom bloom in 2019 has been associated with high silicate concentrations in Kongsfjorden (Assmy et al., 2023). A *Phaeocystis* spring bloom has been suggested to have used up NOx before silicate, facilitating the dominance of diatoms.

Also Ramfjorden, a fjord with no tidewater glaciers, experienced a distinct summer bloom in July 2019, when Chl-a exceeded concentrations found during the spring bloom (Coguiec et al., 2021). The 2019 summer bloom in Ramfjorden was dominated by the harmful hapto-phyte *Chrysochromulina leadbeateri*, which led to the loss of 100 million USD in salmon farms in northern Norway (Aalto et al., 2023). With increased river runoff the fjord was strongly stratified leading to a stable euphotic zone with sufficient light for photosynthesis (Aalto et al., 2023; Grann-Meyer, 2020; John et al., 2022). John et al., (2022) suggested that high levels of river runoff was also a major source of terrestrial organic nitrogen, which was taken up by the mixotrophic *C. leadbeateri* to produce the harmful algae summer bloom (John et al., 2022).

Considering the findings in Isfjorden and Ramfjorden, we suggest that terrestrial nutrient input may occasionally be as important as subglacial upwelling for resupplying nutrients in summer. However, the runoff's nutrient or organic matter concentrations highly depend on the catchment properties (McGovern et al., 2020) and may not lead to summer blooms every year (e.g., Isfjorden, Kongsfjorden). However, many studies, including the RDA of this manuscript, only consider

inorganic nutrients and do not find evidence for terrestrial nutrient input influencing phytoplankton dynamics. Despite the absence of abundant inorganic nutrients from glacially induced upwelling, we suggest that catchments may supply enough organic nutrients to trigger blooms in certain years in both Isfjorden and Ramfjorden. We further suggest that in catchments where the primary runoff passes through rocky terrain inorganic and organic nutrient input are low (e.g., Meire et al., 2023).

Summer communities have also been described to differ between fjords with tidewater and land-terminating glaciers. In Nuup Kangerlua, a fjord with tidewater glacier influence, summer bloom communities are mostly dominated by diatoms (Krawczyk et al., 2015). In contrast, communities in RAM and IsA (2012–2014), where tidewater glacier do not play a role, are mostly dominated by flagellates under non-bloom conditions. Flagellate-dominated summer communities have also been found in other Arctic fjords (e.g. Ameralik, Meire et al., 2023). Many flagellates are capable of efficient mixotrophic carbon and nutrient acquisition, along with the ability to swim and exploit these micro-gradients of nutrients (Li et al., 2009), which can be an advantage in light- and nutrient-limited systems. We also found summer blooms dominated by flagellates in systems with low inorganic nutrient concentrations, are typical for microbial loop dominated systems (Stoecker and Lavrentyev, 2018). This indicates that organic nutrients and re-generated ammonia are playing an important role in driving the dominance of potentially mixotrophic flagellates (e.g., RAM, Mitra et al., 2014). Interestingly, diatom-dominated summer blooms were observed in the 1970 s in Ramfjorden, a fjord with no glacial influence. We suggest that systems with a vegetated catchment (Ramfjorden) are very different from mostly rocky catchments (e.g., Ameralik), by supplying more organic nutrients and less light-absorbing sediments in some years, which then allows diatom summer blooms.

Besides nutrient limitation, grazing pressure may limit phytoplankton biomass in summer. In Nuup Kangerlua, Isfjorden, and to a lower degree in Ramfjorden, grazer abundances were higher during the summer bloom period. In Nuup Kangerlua, a summer phytoplankton bloom with high average primary production but low Chl-a concentrations was often associated with higher grazer abundances (Fig. S10). Higher grazing pressure can best explain this high production-low biomass period (Arendt et al., 2010; Hegseth et al., 2019; Tang et al., 2011). An increase in abundance of grazers concentrated in a strongly stratified surface layer leads to strong grazing pressure and a fast turn-over of rapidly produced Chl-a biomass (Behrenfeld, 2010). In Isfjorden, both primary production and Chl-a decreased in summer, indicating that grazing pressure combined with nutrient depletion, may be important for the termination of the summer bloom. Also, in other Arctic fjords grazing pressure has been discussed as a key driver for the low summer biomass (e.g., Kongsfjorden, Hegseth et al., 2019; Assmy et al., 2023). However, in Ramfjorden grazer abundances were relatively low, suggesting low grazing pressure. Thus, it appears that grazing pressure is not a universal driver reducing summer Chl-a biomass.

An increase in this primary production further leads to a quick reduction in nutrient concentration, manifesting as high production-low nutrient conditions (Olofsson et al., 2021). The increase in NOx concentrations in NK occurred only gradually after the onset of subglacial upwelling (shown as increasing stratification). This delayed increase suggests that primary producers inside the fjord used the available NOx as soon as stratification began, keeping nitrate concentrations low in the surface water.

Arctic fjords are changing rapidly with climate change. Higher temperatures lead to increased glacial melt and retreat, potentially transforming marine-terminating glaciers into land-terminating glaciers. Together with increased precipitation, this leads to increased terrestrial runoff. With retreating glaciers and increasing runoff, greening of land vegetation has been observed (Jia et al., 2003, 2009; Zhang et al., 2018). In Nuup Kangerlua, where subglacial upwelling is the key source of summer nutrient replenishment, a retreat of tidewater

glaciers to land would lead to a reduction in summer nutrient supply and a potential lack of summer blooms dominated by flagellates (Meire et al., 2023). While terrestrial runoff does contribute to the supply of nutrients in Ramfjorden and Isfjorden, we suggest that this would likely be a minor source in Nuup Kangerlua, due to the mostly glaciated and rocky catchment. Conversely, in Isfjorden and Ramfjorden increased summer runoff may also increase the influx of terrestrial nutrients. However, an increase in terrestrial plant biomass may lead to competition for terrestrial inorganic nutrients taken up in the catchment (Søgaard et al., 2023). But organic matter which is ultimately available to fjord primary producers may become more important for fueling future summer blooms of mixotrophic flagellates. While light is typically not limiting in summer, suspended sediments from terrestrial runoff have the potential to influence the marine light regime (Konik et al., 2021).

(iii) Autumn bloom

Autumn blooms have often been described from north Atlantic open ocean studies (Assmy and Smetacek, 2009; Friedland et al., 2016; Martinez et al., 2011). At this time of the year, decreasing stratification and increasing wind allows mixing and upwelling of nutrients into the euphotic zone. In higher latitudes, however, autumn mixing may occur after the light-sufficient growing season. No distinct autumn bloom was apparent in either Isfjorden or Nuup Kangerlua. However, the extended summer/autumn bloom in NK, with relatively high Chl-a until the end of the growth period, indicates a continued supply of summer nutrients from subglacial upwelling (Nuup Kangerlua) as suggested by Juul-Pedersen et al. (2015).

In Ramfjorden a distinct autumn bloom was present in September/October following a low Chl-a period in late summer. This autumn bloom has been detected in all autumns measured (Eilertsen and Taasen, 1984; Vonnahme et al., 2022), suggesting this to be a common feature. However, late meltwater runoff or the absence of autumn storms may drive interannual variability in the magnitude of the autumn bloom. In addition, grazer abundances and potentially grazing pressure are highest in autumn (Coguiec et al., 2021), making mixing not only important for resupplying nutrients, but also for decreasing grazing pressure (Behrenfeld, 2010). The absence of an autumn bloom in Isfjorden may be due to the shorter growing season, which means that the water column stays stratified until light becomes limiting unless air temperatures drop earlier than usual. However, in Nuup Kangerlua the growing season is longer than in Ramfjorden and a distinct autumn bloom is still lacking. We suggest that the main reason for the lack of a distinct autumn bloom is that the long summer blooms last until autumn, masking the autumn bloom and potential effects of wind upwelling in autumn. In addition, not only the growing season, but also the melting season is longer in NK, which means a longer period of strong surface stratification. In addition, tidal mixing, and summer supply of nutrients from subglacial upwelling would mean that autumn mixing may be less important than subglacial upwelling and tidal mixing. However, the complete lack of an autumn bloom in the neighboring Ameralik fjord indicates that autumn blooms driven by wind mixing may also be negligible in NK (Meire et al., 2023). The autumn bloom community at Ramfjorden consists of various diatoms, such as *Skeletonema* spp., *Pseudo-nitzschia* spp., and *Chaetoceros* spp. (Eilertsen et al., 1981, Table 2 and Fig. 5). While nutrients can be replenished in autumn, light becomes more limiting due to shorter days and a deeper mixed layer depth. Thus, species adapted to low-light and high nutrient conditions are best adapted to autumn blooms, making them distinctly different from spring diatom blooms in their composition. *Skeletonema costatum* has been described to be well adapted to low-light conditions (Shoman and Akimov, 2022) and is indeed one of the most abundant species in the Ramfjorden autumn blooms (Fig. 4). Towards the end of this bloom dinoflagellates (e.g., *Scripsiella* spp.) became more abundant in Ramfjorden and Balsfjorden (Eilertsen et al., 1981). The mixotrophic or heterotrophic capabilities of dinoflagellates may allow them to

Table 2
Dominating species (>20 %) observed in highest relative abundance at the beginning and end of the three periods.

Station	Spring		Summer		Autumn	
NK	**Beginning** *Phaeocystis pouchetii, Chaetoceros* spp., *Thalasiossira* spp.	**End** *Phaeocystis pouchetii, Chaetoceros* spp.	**Beginning** *Chaetoceros* spp. *Thalassiosira* spp., *Skeletonema* spp.	**End** *Chaetoceros* spp., *Pseudo-nitzschia* spp.	**Beginning** Extended summer bloom: *Chaetoceros* spp., Pennales, *Skeletonema* spp.	**End** Extended summer bloom: *Chaetoceros* spp., *Thalasiossira* spp.
RAM	*Chaetoceros socialis, Phaeocystis pouchetii, Chaetoceros* spp., *Alexandrium* spp.	Gymnodiniales, Flagellates	**1970 s:** *Pseudo-nitzschia* spp., *Chaetoceros* spp., Dinoflagellates, Gymnodiales **2019:** *Chrysochromulina leadbeateri*	**1970 s:** *Pseudo-nitzschia* spp., *Chaetoceros* spp., Dinoflagellates, *Scripsiella* sp., Gymnodiniales	*Pseudo-nitzschia* spp. Dinoflagellates, *Chaetoceros* spp., *Scripsiella* spp., Gymnodiniales	*Skeletonema* spp., *Chaetoceros* spp., *Pseudo-nitzschia* spp.
IsA	**2012:** *Phaeocystis pouchetii Chaetoceros* spp.*Thalasiossira* spp. **2013:** *Fragillariopsis* spp., Flagellates, *Chaetoceros socialis* (pre bloom) **2014:** *Phaeocystis pouchetii, Flagellates, Gymnodiniales*	**2012:** *Phaeocystis pouchetii*, Flagellates **2013:** Flagellates, *Fragillariopsis* spp. **2014:** *Chaetoceros* spp., Flagellates, *Thalasiossira* spp., *Fragillariopsis* spp.	No summer blooms in 2012–2014	no summer blooms in 2012–2014	no autumn blooms	no autumn blooms

dominate when light conditions are too low for diatom blooms. Similarly in NK, a transition from autumn to a winter microplankton community is typically observed around October, where *Thalassiosira* spp. and *Thalassionema nitzschioides* along with ciliates and dinoflagellates contribute more to the species composition in a low biomass community (Krawczyk et al., 2015).

With future climatic changes, autumn blooms experiencing increased and extended runoff would mean that the water column stays stratified until the end of the growing season and autumn blooms driven by autumn mixing may disappear. With the associated decrease in phytoplankton biomass, the high autumn abundances of zooplankton in Ramfjorden would likely also be affected. However, increased frequencies of storms may counteract this mechanism to some extent and lead to periodical mixing of the water column, potentially triggering short-term autumn blooms (Ardyna et al., 2014). Additionally, an increase in AW inflow due to climate change could also lead to increasing autumn blooms in the Arctic, due to an increase in nutrient inflow with this AW, and destabilization of the water column (Orkney et al., 2022).

5. Conclusions

Our study provides a comprehensive comparison of the seasonal dynamics of phytoplankton blooms in three distinct Arctic fjords: Nuup Kangerlua (Greenland), Ramfjorden (Norway), Isfjorden (Svalbard).

The findings highlight that light availability, nutrient supply, and grazing pressure are key factors shaping the timing, magnitude, and community composition of these blooms. While all fjords exhibited pronounced spring blooms, the presence and characteristics of summer and autumn blooms varied across fjords. The study suggests that terrestrial runoff and subglacial upwelling can resupply nutrients to surface waters fueling summer blooms across the latitudinal gradient. However, drivers of summer blooms are different between fjords and between years and local environmental and climatic variability need to be understood for predicting future summer blooms in Arctic fjords. Autumn blooms are fueled by nutrient resupply through wind mixing in a mixed water column, but daylight sets a temporal constraint on how long an autumn bloom can continue. As climate change continues to reshape the environment, it is important to understand bloom dynamics and their local and global drivers to predict cascading effects on higher trophic levels and local communities and livelihoods.

Author contributions

CC and TV wrote and designed the idea behind this study. Field sampling from NK at Greenland was conducted by TJP, MW and TV, from IsA on Svalbard was conducted by AV, CC, JS and several UNIS students. Field sampling at RAM in Northern Norway was conducted by RG and TV. DK carried out taxonomic analyses of protist samples from NK. Figures were plotted by both TV and CC. Statistical analyses were carried out by CC. All co-authors contributed to data interpretation and to the writing of the manuscript.

CRediT authorship contribution statement

Cheshtaa Chitkara: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Thomas Juul-Pedersen:** Writing – review & editing, Supervision. **Diana Krawczyk:** Writing – review & editing. **Janne E. Søreide:** Writing – review & editing, Methodology. **Anna Vader:** Writing – review & editing, Supervision, Project administration. **Rolf Gradinger:** Writing – review & editing. **Mie HS Winding:** Writing – review & editing. **Tobias R Vonnahme:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data made available through links mentioned. Links not mentioned will be published, but can be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2024.103317.

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