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RESEARCH ARTICLE

Environmental controls of autotrophic biofilm biomass and community composition in subarctic lakes and streams in Greenland

Sanne Mariël Moedt,[1] **Tenna Riis**,[2] **Dean Jacobsen**,[1] **Ole Geertz-Hansen**,[3] **Kenneth Thorø Martinsen**,[1] **Kirsten Seestern Christoffersen**[1,4*]

[1]Department of Biology, University of Copenhagen, Copenhagen, Denmark; [2]Department of Biology, Arctic Research Center, Aarhus University, Aarhus, Denmark; [3]Greenland Institute of Natural Resources, Nuuk, Greenland; [4]Arctic Biology Department, University Centre in Svalbard, Svalbard, Norway

Abstract

Photosynthetic biofilms are key components of Arctic freshwater ecosystems, supporting primary production and forming the base of aquatic food webs. While several environmental factors regulating biofilms are known, their relative importance and connection to catchment characteristics across different Arctic ecosystems remain unclear. This study assessed epilithic biofilm biomass and autotrophic community composition in lakes and streams near Narsaq, South Greenland. Lake biofilms were dominated by cyanobacteria, with autotrophic biomass positively associated with catchment greenness and water conductivity. In streams, biofilms primarily comprised diatoms and green algae, with autotrophic biomass linked to phosphate, pH, and temperature. Total biofilm biomass in lakes was also related to catchment greenness and conductivity, while no consistent environmental drivers were found for stream biomass. These findings underscore how environmental controls on biofilm structure differ between lentic and lotic systems. As climate warming intensifies tundra greening and alters nutrient regimes, autotrophic biofilm biomass is likely to increase, potentially affecting food web dynamics and carbon cycling in Arctic freshwater ecosystems. Our findings advance the understanding of Arctic freshwater biofilm dynamics and their sensitivity to climate-driven changes.

Biofilms are complex communities of algae, bacteria, and fungi embedded in extracellular matrices that play critical roles in freshwater ecosystems by driving nutrient cycling, contributing to primary production, and structuring habitats (Bonilla et al. 2005; Quesada et al. 2008; Brandani et al. 2022). Epilithic biofilms, which grow on submerged surfaces such as rocks, are especially important in both lentic and lotic systems, where they underpin food webs and enhance ecosystem productivity (Battin et al. 2016; Pastor et al. 2021).

In high-latitude and high-altitude environments, epilithic biofilms serve as a key food source for invertebrates and often dominate basal resource pools (Brett et al. 2017; Vadeboncoeur and Power 2017). The photoautotrophs within these biofilms are predominantly composed of diatoms, green algae, and cyanobacteria (Quesada et al. 2008; Sudlow et al. 2023), with cyanobacteria generally dominating lentic systems due to their ability to thrive in stable, ultra-oligotrophic conditions (Rautio et al. 2011; Lionard et al. 2012; Mohit et al. 2017), while diatoms and green algae are more common in lotic systems, where their capacity for rapid growth and strong substrate attachment allows them to take advantage of high light availability and flowing water (Quesada et al. 2008; Gettel et al. 2013). These extreme systems are characterized by low temperatures, high ultraviolet radiation (UVR), and nutrient-poor conditions (Quesada et al. 2008; Battin et al. 2016; Sudlow et al. 2023). Beyond these key regulating factors, epilithic biofilm biomass and composition are influenced by a suite of interacting controls, including dissolved organic matter (DOM), grazing dynamics, hydrological disturbance, and substrate characteristics (Stoodley et al. 1999; Battin et al. 2003; Lang et al. 2015; Melissa et al. 2020; Huttunen et al. 2025).

*Correspondence: kchristoffersen@bio.ku.dk

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One of the primary drivers influencing epilithic biofilms in Arctic lakes and streams is the low water temperature (Docherty et al. 2018; Myrstener et al. 2018; Pastor et al. 2021; Moedt et al. 2025), which hampers microbial activity and affects metabolic rates and nutrient cycling. Light availability is another critical growth factor for photosynthetic biofilms (Vigneron et al. 2018; Hofmann et al. 2020; Weaver and Jones Jr. 2022). The subarctic winter period has low or no light intensity for 2–3 months, while the summer has excessive light exposure, which can lead to photo-inhibition. Both extremes will influence the composition and productivity of the autotrophic biofilm communities (Quesada et al. 2008). Catchment characteristics such as steepness and vegetation cover may also affect biofilms via changes in water nutrient content. Harms et al. (2016) have shown a positive correlation between catchment slope and nitrate (NO_3^-) concentrations in streams, and Riis et al. (2023) found a positive correlation between catchment vegetation cover and stream NO_3^- concentrations. Higher NO_3^- concentrations have been shown to promote stream biofilm accumulation in Arctic areas (Myrstener et al. 2018; Pastor et al. 2020) and Pastor et al. (2021) showed that biofilm chlorophyll *a* (Chl *a*) concentrations are positively associated with vegetation cover. However, while individual factors within high-latitude and high-altitude systems, such as temperature (Docherty et al. 2018; Moedt et al. 2025), light availability (Hofmann et al. 2020), and nutrient input (Myrstener et al. 2018; Pastor et al. 2020; Moedt et al. 2025; Huttunen et al. 2025), are known to influence biofilm biomass and composition, the interactions and relative importance of these controls and the indirect links to catchment characteristics such as catchment topographic slope and vegetation greenness remain poorly understood. This is particularly true for subarctic regions where climate-driven environmental changes are large (Huttunen et al. 2025; Moedt et al. 2025).

South Greenland represents a compelling study system for addressing these knowledge gaps. As a transitional zone between temperate and Arctic climates, this subarctic area is experiencing rapid environmental change (Rantanen et al. 2022), including glacier retreat (Sellevold and Vizcaíno 2020), greening of the terrestrial environment (Zhang et al. 2018), increased opportunities for agriculture (Gudmundsdottir et al. 2011; Bichet et al. 2013), and pressures from potential mining activities (Marks and Markl 2015). These shifts are altering nutrient dynamics and hydrological regimes in freshwater systems, with unknown consequences for epilithic biofilms.

To improve our understanding of how biofilms are regulated by environmental conditions in extreme ecosystems, we investigated lakes and streams across an elevational gradient in South Greenland. Our study aims to identify the relative influence of key environmental drivers, both direct (e.g., light, temperature, nutrients, hydrology) and indirect (e.g., catchment characteristics), on biofilm biomass and composition. Specifically, we hypothesized that (1) higher elevations reduce biofilm biomass due to shorter ice-free seasons and terrestrial-aquatic connectivity, and that (2) catchment slope and vegetation greenness increase biofilm biomass by enhancing nutrient and solute runoff, with higher nutrient concentrations supporting greater biomass in these nutrient-limited systems. Additionally, we predicted that (3) higher current velocity negatively affects stream biofilm accumulation due to mechanical removal at high current velocity. Furthermore, we expected to confirm earlier findings that (4) community composition differs between habitats, with cyanobacteria dominating lake biofilms and diatoms and green algae being more prevalent in streams.

Methods

Study site

During August 2022, six locations along the Narsaq River and two of its lake-fed tributaries, as well as nine lakes in the Narsaq region in South Greenland, were sampled (Fig. 1). The local weather conditions in South Greenland are influenced by the North Atlantic Ocean and by the Greenland Ice Sheet. Narsaq lies within the subarctic climate zone, as defined by Conservation of Arctic Flora and Fauna (CAFF; Culp et al. 2021). The area has cool summers and cold winters and is located approx. 25 km from the edge of the ice sheet. The Narsaq region (60°54′44″N 46°02′55″W), encompassing Kuannersuit and Killavaat Alannguat, is rich in rare-earth minerals (Hutchison et al. 2021). An extensive driven cattle farm with pastures is situated along the lower part of the Narsaq River, and cattle roam freely in the mountains surrounding the Narsaq River, which will likely contribute to disturbances in this area. Lakes studied in the area south of Narsaq are not affected by farming. Annual mean temperatures are between 0 and 3°C, and mean summer temperature (July–August) varies from 6 to 9°C (Danish Meteorological Institute, http://research.dmi.dk/publications/other-publications/reports/). Day length in June is around 19 h, and in December around 5.5 h. Annual precipitation is between 250 and 800 mm. The study area spans a marked elevation gradient, transitioning between two distinct climatic zones: low-lying areas, dominated by herbaceous vegetation and willows, and higher terrain above 300 m above sea level (a.s.l.), where vegetation becomes sparse. For clarity, we refer to these as low and high elevation sites, respectively. At the higher end of the Narsaq valley lies a small glacier, which feeds the Narsaq River.

Physico-chemical parameters

Water was sampled from 0.5 to 1 m depth in the center of the lake and mixed in a bucket. At the stream sites, a water sample was collected from the middle of the stream and placed in a bucket. At every site, we measured water temperature and conductivity in situ using a YSI Multi Sonde. Water samples for water chemistry were filtered in the field. For

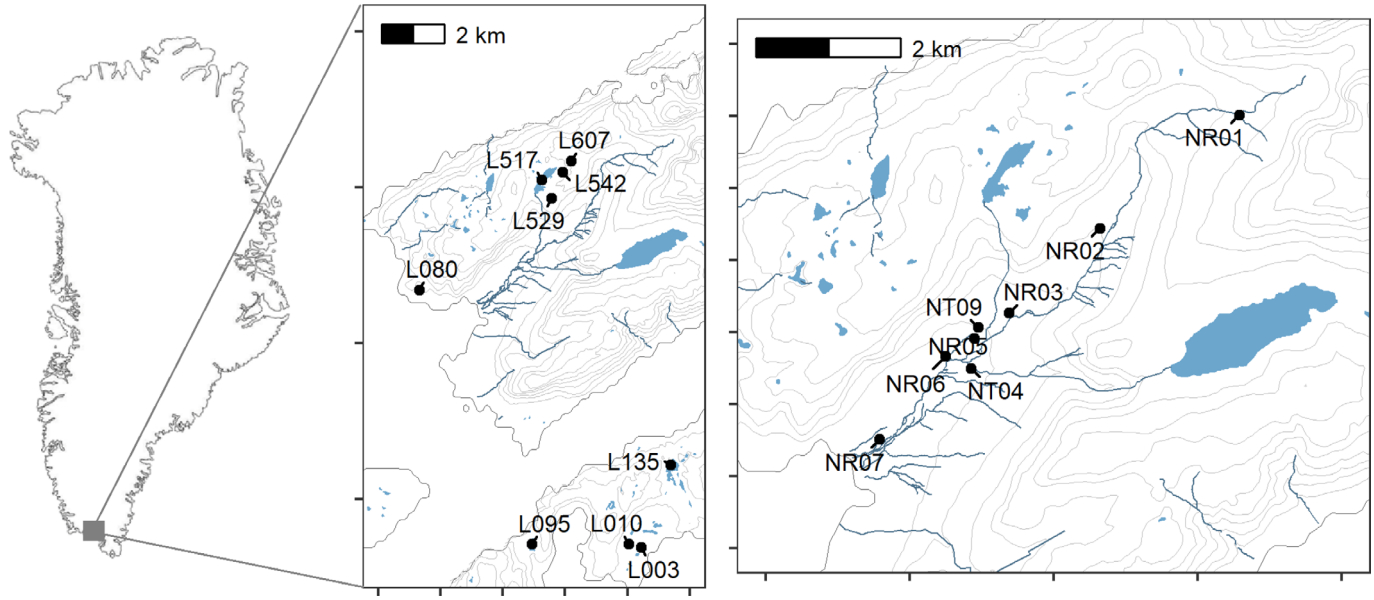

Fig. 1. Map of the Narsaq area in South Greenland with lakes (left) and stream sites (right). Name codes for the lakes are based on the elevation measurements from a previous study that took place in the 1970s (Rose-Hansen et al. 1977). Each topographic line on the map indicates a 100-m change in elevation.

nutrient analyses, samples were filtered through a membrane filter (Supor 200 PES, Pall Corporation, Port Washington, New York, United States), and other samples (excluding alkalinity) were filtered through pre-combusted glass fiber filters (GF/F, Whatman, United Kingdom). Nutrient samples were frozen until analysis, while alkalinity samples were kept in the fridge at 5°C. In the lab, pH and alkalinity were measured. For alkalinity, a 50 mL unfiltered water sample was analyzed by titration with 0.01 M HCl (TitraLab® TIM850 Titration Manager with TitraLab® ABU52 Biburette). Samples for dissolved organic carbon (DOC) and total nitrogen (TN) were analyzed on a Shimadzu TOC Analyzer (TOC-VCSH). Total phosphorus (TP) in water was analyzed spectrophotometrically following Danish standard methods (DS-291_ISO 6878:2004). Samples for dissolved major ions were analyzed using an ICP-MS (PerkinElmer Instruments, Optima 2000 DV). Nutrients (NO_3^-, NH_4^+ and PO_4^{3-}) were analyzed using a Lachat QC-8500 Flow Injection Autoanalyzer (colorimetric analysis; Lachat Instruments, Loveland, Colorado, US; APHA, 2005).

Epilithic biofilms

Epilithic biofilm samples were collected at each site by randomly picking three or four flat stones that were placed in a tray. A photo was taken of the tray together with measuring tape, which was later used to quantify the surface area of the stones using the program ImageJ. Subsequently, the biofilm was removed from the light-facing surface of the stone using a toothbrush with a known volume (< 100 mL) of lake or stream water. The resulting slurry was transferred to a bottle, which was kept in the dark until further processing. Three replicate slurries were collected at each site along the reach of a stream or in the littoral zone of a lake.

Within 6–10 h a small amount (5–15 mL) of slurry from individual samples was filtered onto pre-combusted GF/F filters (0.7 μm, Whatman, UK) for later measurements of Chl *a*, ash-free dry weight (AFDW), and carbon to nitrogen ratio (C : N). Next, the three replicate slurries were mixed, and a small amount (5–15 mL) was filtered onto a pre-combusted GF/F filter for pigment analysis using High-Performance Liquid Chromatography (HPLC). All filters were wrapped separately in aluminum foil and frozen at −20°C until further analyses. The remainder of the mixed slurries was preserved with Lugol's solution and stored in the dark for microscopic analysis. In the laboratory, filters for Chl *a* analysis were moved to a vial containing ethanol and left in darkness overnight for pigment extraction. Subsequently, the extracted pigments were quantified using a spectrophotometer at wavelengths of 665 and 750 nm. These measurements were used to calculate Chl *a* concentrations per cm^2 of stone surface. Ash-free dry weight filters underwent a two-step process. Initially, they were dried at 60°C for 48 h, and their dry weight was measured. Following this, the filters were put in a muffle oven at 480°C for 5 h, after which they were re-weighed. These weight measurements were then used to calculate the biofilm AFDW cm^{-2} of stone surface. The autotrophic index (AI) was determined by calculating the ratio of AFDW (mg cm^{-2}) to Chl *a* (mg cm^{-2}). An elevated AI (exceeding 200) suggests substantial presence of non-autotrophic (e.g., heterotrophic) or non-living organic material, while a low AI indicates a relatively large contribution from the autotrophic community (Steinman et al. 2017).

Biofilm content of C and N was determined in slurry material collected on a GF/C filter by catalytic combustion at 900°C on an HCN analyzer (Elementar vario EL cube). Due to insufficient amount of biomass per filter, measurements of biofilm phosphorus (P) were not done.

One GF/F filter for each site (nine lake and eight stream samples) was analyzed at the Danish Hydraulic Institute (DHI), Hørsholm, Denmark (www.dhigroup.com), for pigment content using HPLC. There, the samples were extracted with 95% acetone containing vitamin E (internal standard), sonicated in an ice-cold bath for 10 min, and left to extract at 4°C for 20 h. The Van Heukelem and Thomas (2001) method was used for the analysis. Fucoxanthin was used as a biomarker for diatoms, aphanizophyll and zeaxanthin for cyanobacteria, and neoxanthin, violaxanthin, and Chl *b* for green algae. Other pigments were detected as well. From DHI, we received the CHEMTAX results of the different phototrophic autotrophs in μg Chl *a* L^{-1} of biofilm slurry. Using biofilm slurry volume, volume of added lake or stream water to the slurry, and stone surface area, we calculated the Chl *a* concentration cm^{-2} for each group. Unfortunately, we lack a photo of one tray at L542 and at L607. Therefore, we calculated the mean surface area of the other trays to estimate the surface area of the stones in the missing trays. This mean value was used to calculate Chl *a* concentrations cm^{-2} of the different algae samples.

Autotrophic taxa were determined qualitatively using a microscope at 100- and 400-times magnification. Prior to analysis, each sample was mixed by slowly turning the bottle around for 30 s. Then, using a pipette, a small subsample was taken and placed on a microscope slide, which was subsequently covered with a glass cover slip and placed under the microscope. Common taxa were identified to genus level, or to a different level that was possible, using multiple identification guides (Krammer and Lange-Bertalot 1986; Komárek and Anagnostidis 1999, 2005; John et al. 2011). The analysis of each sample took around 2 h, during which several subsamples were inspected.

Watershed delineation and satellite imagery

Watershed boundaries for lakes and streams were delineated using a digital elevation model (DEM) with a resolution of 2 m (SDFE 2022). Lake polygons were obtained from SDFE (2022) or created manually using high-resolution satellite imagery. The DEM was preprocessed using least cost breaching (Lindsay and Dhun 2015) and filling of depressions (Wang and Liu 2006). Flow directions were determined using the D8 algorithm (O'Callaghan and Mark 1984) and were used to delineate watershed boundaries. We used the algorithms implemented in Whitebox Tools to perform DEM processing and watershed delineation (Lindsay 2016). We quantified terrestrial vegetation greenness as normalized difference vegetation index (NDVI), hereafter also referred to as catchment greenness. The NDVI was determined from surface reflectance at 10 m resolution using Sentinel-2 satellite imagery. We used atmospherically corrected, Sentinel-2 B, level 2A imagery captured August 22, 2022 (Copernicus Sentinal Data 2023, ID: S2B_MSIL2A_20220822T143749_N0400_R039_T23VMH_20220822T172435). Finally, we determined the area and extracted the mean elevation, slope, and NDVI for each watershed. Spatial data analysis also used GDAL (GDAL/OGR contributors, 2022), the terra (Hijmans et al. 2023), exactextractr (Baston 2022), and sf (Pebesma 2018) R-packages (R Core Team 2022).

Data processing and statistical analyses

The dataset consists of biofilm characteristics (Chl *a*, AFDW, AI, and C : N), autotrophic community composition, and physico-chemical characteristics. ANOVAs were performed to test the effect of lake elevation on biofilm characteristics and stream type (Narsaq River and tributary) on biofilm characteristics. To identify correlations among independent variables, we conducted a Spearman Rank correlation analysis for all independent variables in lakes and streams, respectively. To identify the main environmental drivers shaping epilithic biofilms in the lakes and streams, we identified linear relationships between biofilm characteristics and environmental predictors using stepwise multiple linear regression analysis from R stats package (R Core Team 2022). Forward selection was used to select predictors. The response variable was log-transformed to approach linearity where necessary. Model selection was based on the Akaike information criterion (AIC). Normality of residuals was tested with a Shapiro–Wilk test, and homogeneity of variances was checked visually. Explanatory variables were tested with a permutational ANOVA, and only variables with a p-value < 0.1 were included in the analysis.

Results

Lakes

Physico-chemical and catchment characteristics

Water temperature ranged from 13.1 to 15.5°C (Table 1). Conductivity levels were higher in lakes at low elevation (38–60 μS cm^{-1}), that is, below 300 m, than at high elevation (16–36 μS cm^{-1}; ANOVA, $F = 10.68$, $p = 0.014$). pH ranged from 6.85 to 7.39 and alkalinity from 0.082 to 0.356 mEq L^{-1}. Lakes at low elevation had higher NH_4^+ concentrations, namely 13–62 compared to 5–17 μg N L^{-1} at high elevation (ANOVA, $F = 8.77$, $p = 0.02$). Phosphate concentration was lowest in L135 (1 μg P L^{-1}) and highest in L542 (15 μg P L^{-1}), and NO_3^- concentration was lowest in L010 (1 μg N L^{-1}) and highest in L080 (18 μg N L^{-1}). Total phosphorus (TP) was lowest in L010, L095, and L607 (all 8 μg P L^{-1}) and highest in L542 (28 μg P L^{-1}). Total nitrogen (TN) was lowest in L135 (73 μg N L^{-1}) and highest in L607 (366 μg N L^{-1}). Dissolved organic carbon (DOC) levels were lowest in L529 (0.83 mg C L^{-1}) and highest in L095 (3.15 mg C L^{-1}), and silica levels

Table 1. Physico-chemical characteristics of nine lakes organized according to elevation (low to high), and of the six Narsaq River (NR) sites organized from up- to downstream and two lake-fed tributaries (NT) in the Narsaq area. N.a. = not available.

	Velocity ($m\ s^{-1}$)	Water temperature (°C)	Conductivity ($\mu S\ cm^{-1}$)	pH	Alkalinity ($mEq\ L^{-1}$)	NH_4^+ ($\mu g\ N\ L^{-1}$)	PO_4^{3-} ($\mu g\ P\ L^{-1}$)	NO_3^- ($\mu g\ N\ L^{-1}$)	TP ($\mu g\ L^{-1}$)	TN ($\mu g\ L^{-1}$)	DOC ($mg\ C\ L^{-1}$)	Si ($mg\ L^{-1}$)
Lakes												
L003		13.7	53.3	6.95	0.109	62	3	10	9	186	2.74	0.11
L010		15.4	44.0	6.96	0.098	28	3	1	8	161	2.84	0.15
L080		13.5	60.2	7.22	0.356	45	3	18	15	169	2.05	0.59
L095		12.6	42.5	6.85	0.113	40	2	3	8	275	3.15	0.09
L135		13.4	38.0	7.39	0.320	13	1	3	9	73	1.39	0.12
L517		14.2	35.8	7.15	0.141	5	3	5	10	105	1.17	0.34
L529		15.5	26.6	7.14	0.101	5	3	7	10	88	0.83	0.36
L542		13.4	33.4	7.21	0.254	5	15	3	28	111	1.21	0.52
L607		13.1	15.6	7.05	0.082	17	4	4	8	366	2.68	0.11
Streams												
NR01	0.60	2.6	38.7	7.41	0.261	5	3	27	9	59	0.22	0.87
NR02	n.a.	5.5	46.2	7.40	0.281	5	6	15	17	66	0.32	0.78
NR03	0.80	5.8	52.4	7.33	0.282	44	11	95	22	79	0.47	1.07
NR05	0.80	6.8	51.8	7.19	0.270	5	8	15	16	57	0.41	1.24
NR06	n.a.	7.2	52.3	7.15	0.286	5	6	11	17	69	0.47	1.27
NR07	0.79	7.4	62.9	7.39	0.342	10	6	7	13	64	0.40	1.60
NT04	0.80	9.4	54.6	7.28	0.284	5	4	25	7	74	0.50	1.51
NT09	0.16	8.8	50.8	7.42	0.282	5	11	6	17	62	0.80	0.84

were lowest in L095 (0.09 mg L^{-1}) and highest in L080 (0.59 mg L^{-1}). Lake area ranged from 4981 (L607; Table 2) to 202,040 m^2 (L517), and catchment area from 0.08 (L529) to 1.84 km^2 (L135). Mean catchment slope was least steep at L607 (14°) and steepest at L080 (22°), and mean catchment elevation ranged from 115 to 673 m. Finally, mean greenness of the catchment was higher at low elevation than at high elevation (NDVI at 0.61–0.70 and 0.43–0.53, respectively; ANOVA, $F = 50.73$, $p < 0.001$).

Biofilm characteristics

Lake epilithic biofilms were 5–10 mm thick and varied from being brown and slimy to a dark-colored crust. Chlorophyll *a* concentrations ranged from 0.172 to 6.994 $\mu g\ cm^{-2}$ (Fig. 2a; Supporting Information Table S1) and were higher in lakes at low elevation compared to lakes at high elevation (Fig. 2; Table 3, ANOVA, $F = 17.78$, $p < 0.001$; Table 3). Ash-free dry weight was between 0.41 and 9.15 mg cm^{-2} (Fig. 2b; Supporting Information Table S1) and was higher in lakes at low elevation (ANOVA, $F = 6.98$, $p = 0.015$; Table 3). Autotrophic index ranged from 152 to 3196 (Fig. 2c; Supporting Information Table S1). In all lakes, except L080, the index consistently exceeded 200, meaning that the biofilm contains large amounts of non-algal and/or non-living organic material. Lastly, C : N ratios of biofilms ranged from 8.39 to 15.40 (Fig. 2d; Supporting Information Table S1).

Autotrophic community composition

The autotrophic assemblage of the epilithic biofilm in the lakes consisted of cyanobacteria, diatoms, and green algae (Fig. 3). Cyanobacteria were the most abundant group, making up more than 50% of the total autotrophic community biomass in all lakes, except for L542, where it was just under 50% and equal to the biomass of green algae. Total Chl *a* concentrations ranged from 0.50 to 3.30 $\mu g\ cm^{-2}$ (Fig. 3a). While Chl *a* concentrations did differ between lakes at low and high elevation (Table 3), community composition did not (Fig. 3).

The most common cyanobacteria genera within lake epilithic biofilm were *Stigonema*, *Scytonema*, *Dichothrix*, *Nostoc*, *Leptolyngbya*, *Komvophoron*, *Pseudanabaena*, *Phormidium*, and Chroococcales. Common green algal genera were *Bulbochaete*, *Mougeotia*, *Zygnema*, *Ulothrix*, *Cosmarium*, *Euastrum*, and *Desmidium*. Finally, diatom taxa that were present were *Tabellaria flocculosa*, *Cymbella* sp., and several other diatom spp.

Drivers of lake epilithic biofilm biomass

Mean NDVI of the lake catchment was the strongest driver of both biofilm Chl *a* concentrations ($F = 89.28$, $p < 0.0001$; Table 4; Fig. 4b) and AFDW ($F = 15.46$, $p < 0.001$; Fig. 4f). Chlorophyll *a* was also positively related to water conductivity ($F = 8.29$, $p = 0.01$; Fig. 4a). Ash-free dry weight was positively correlated to conductivity as well ($F = 9.27$, $p = 0.0067$; Fig. 5e). Other significant drivers of AFDW were alkalinity

Table 2. Lake area and catchment properties of nine lakes organized according to elevation (low to high), and catchment properties of six Narsaq River (NR) sites organized from up- to downstream and two lake-fed tributaries (NT) in the Narsaq area.

	Lake area (ha)	Mean slope of catchment (°)	Mean catchment elevation (m)	Catchment area (km^2)	Mean NDVI
Lakes					
L003	13.6	15	115	1.68	0.61
L010	76.9	18	148	1.13	0.67
L080	0.9	22	172	0.25	0.68
L095	74.5	20	195	0.62	0.70
L135	182.8	17	285	1.84	0.66
L517	202.0	16	603	1.51	0.53
L529	24.3	14	558	0.08	0.50
L542	0.5	15	635	0.53	0.43
L607	0.7	14	673	0.16	0.47
Streams					
NR01		25	1025	5.17	0.16
NR02		21	822	11.45	0.24
NR03		21	726	14.69	0.27
NR05		20	678	18.58	0.32
NR06		19	626	30.54	0.27
NR07		19	583	34.56	0.31
NT04		17	575	11.04	0.16
NT09		19	567	36.13	0.32

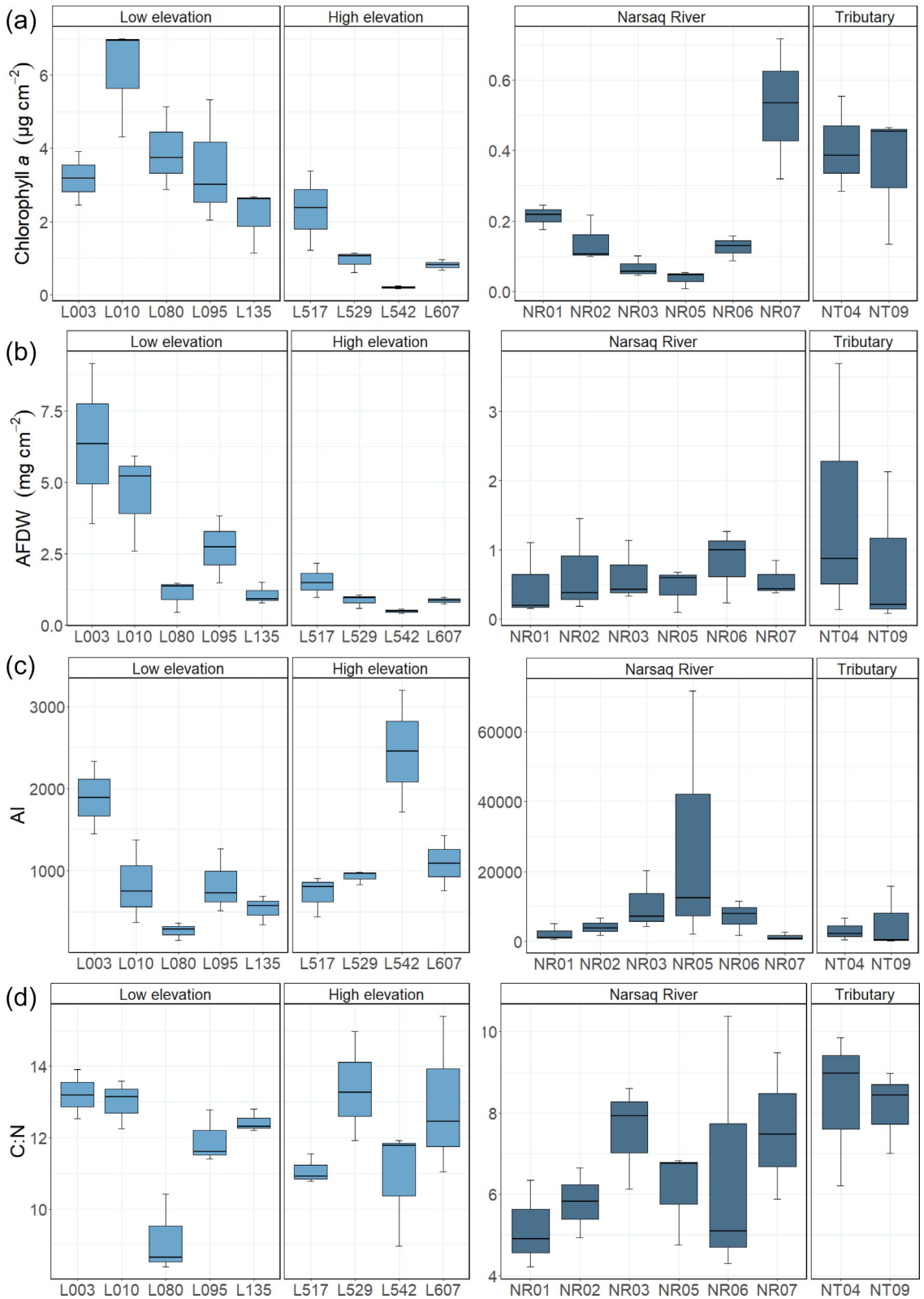

Fig. 2. Mean (**a**) Chl *a* concentrations (μg cm^{-2}, spectrophotometer), (**b**) AFDW (mg cm^{-2}), (**c**) autotrophic index, and (**d**) C : N with standard deviation of epilithic biofilm in the lakes (low and high elevation) and stream sites (Narsaq River from up- to downstream and tributaries). Note the different scale on the Y-axes.

Table 3. ANOVA results for biofilm characteristics (Chl *a*, AFDW, AI, and C : N) at low (< 300 m a.s.l.) and high elevation (> 300 m a.s.l.) for lakes and for different stream types (Narsaq River and tributary). Df = 1 for all.

	F value	*p* value	Interpretation
Lake elevation			
Chl *a*	17.78	0.0003***	Low elevation > high elevation
AFDW	6.98	0.015*	Low elevation > high elevation
AI	2.01	0.17	
C : N	0.04	0.84	
Stream type			
Chl *a*	5.56	0.028*	Tributary > Narsaq River
AFDW	2.48	0.13	
AI	0.46	0.51	
C : N	5.01	0.036*	Tributary > Narsaq River

*$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

($F = 10.38$, $p = 0.0045$; Fig. 4c) and catchment slope ($F = 7.66$, $p = 0.012$; Fig. 4d). Drivers related to the autotrophic index were phosphate ($F = 17.27$, $p < 0.001$; Fig. 4i), mean catchment NDVI ($F = 12.07$, $p = 0.0027$; Fig. 4h), and lake elevation ($F = 6.84$, $p = 0.018$; Fig. 4g). C : N ratios were related to alkalinity ($F = 19.26$, $p < 0.001$; Fig. 4j), conductivity ($F = 9.08$, $p = 0.0064$; Fig. 4l), and catchment slope ($F = 6.80$, $p = 0.016$; Fig. 4k). The correlation analysis among the explanatory variables showed that catchment NDVI was correlated with catchment slope (0.83; Supporting Information Table S3), water conductivity (0.78), and phosphate (0.75) and ammonium concentrations (0.70). Additionally, water conductivity was correlated with ammonium concentrations (0.78) and pH with silica concentrations (0.67). For more correlations, *see* Supporting Information Table S3.

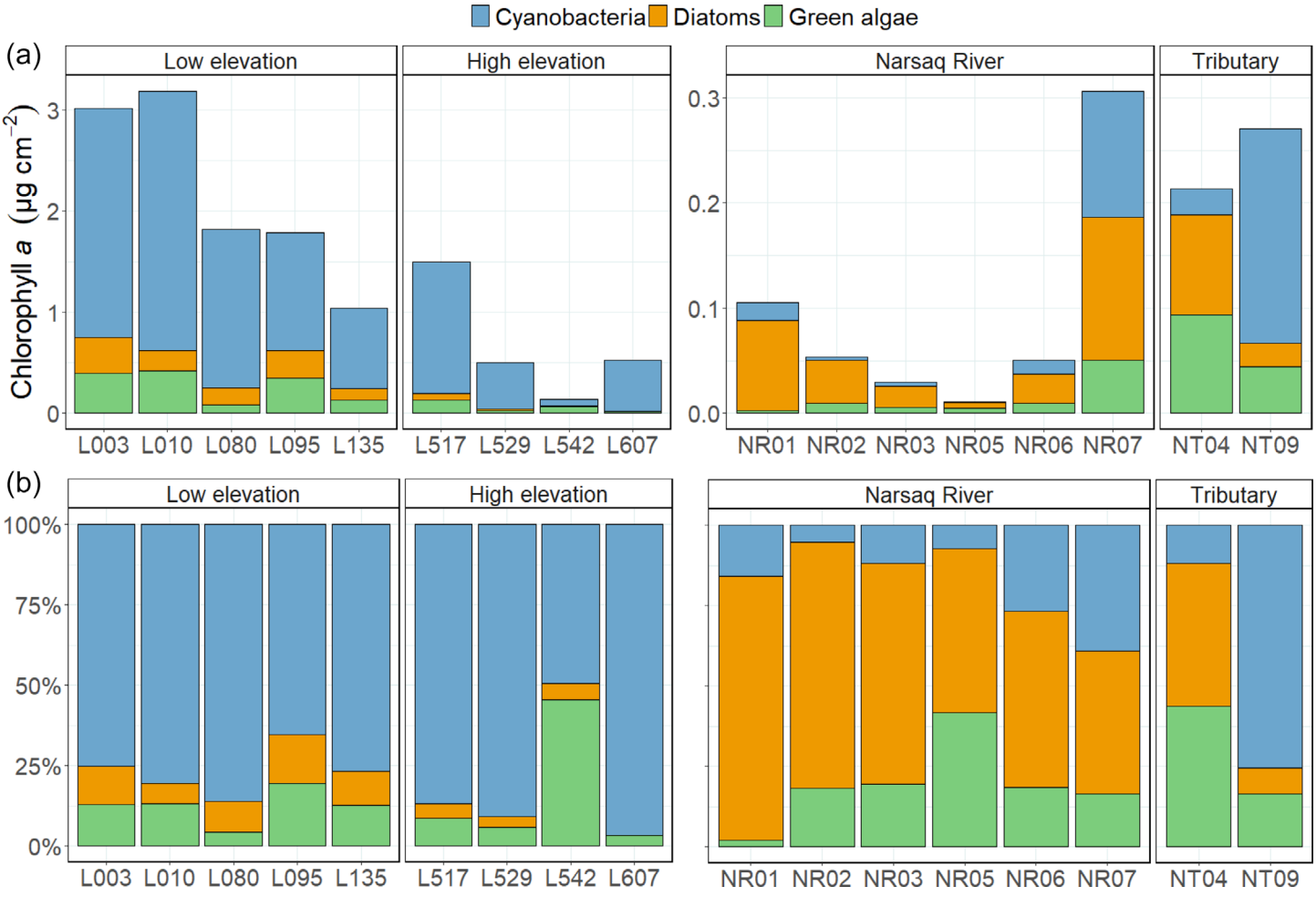

Fig. 3. HPLC results of epilithic biofilm composition in the lakes (left) and stream sites (right) as (**a**) Chl *a* concentrations (μg cm^{-2}) and (**b**) relative abundance (%) of cyanobacteria, diatoms, and green algae Lakes are ordered from low elevation to high elevation and stream sites from up- to downstream with the tributaries separate. Note the different scales on the Y-axes for the Chl *a* concentrations.

Table 4. Multiple linear regression models relating biofilm characteristics in lakes to physico-chemical, catchment, and environmental variables. Data from all lakes are included ($n = 9$). Df = 18 for all. Chl *a* is based on the standard spectrophotometer measurements and is log-transformed.

		Estimate	*t*-value	*F* value	*p* value	Adj. R^2	Model sign.
Chl *a*	Alkalinity	−13.74	3.54	0.095	0.76	0.81	< 0.0001
	Catchment slope	0.16	1.94	3.76	0.068		
	Conductivity	0.05	3.22	8.29	0.01*		
	NDVI	6.44	3.87	89.28	<0.0001***		
	pH	5.99	3.18	1.37	0.25		
AFDW	Alkalinity	−11.76	−3.74	10.38	0.0045**	0.63	0.0001
	Catchment slope	−0.47	−2.77	7.66	0.012*		
	Conductivity	0.11	3.19	9.27	0.0067**		
	NDVI	15.85	2.29	15.46	0.0009***		
	PO_4^{3-}	142.47	1.42	3.07	0.096		
AI	Alkalinity	−1394	−1.22	3.09	0.096	0.60	0.0004
	Conductivity	−7.77	−0.52	0.27	0.61		
	Lake elevation	−3.37	−2.51	6.84	0.018*		
	NDVI	−8254	−2.35	12.07	0.0027**		
	PO_4^{3-}	79,701	2.21	17.27	0.0006***		
C : N	Alkalinity	−3.69	−1.36	19.26	0.0002***	0.55	0.0002
	Catchment slope	−0.30	−2.61	6.80	0.016*		
	Conductivity	−0.08	−2.29	9.08	0.0064**		
	Lake elevation	−0.01	−3.39	0.54	0.47		

*$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Streams

Physico-chemical and catchment characteristics

Stream velocity was lowest at NT09 (0.16 m s^{-1}; Table 1) and highest at NR03, NR05, and NT04 (all 0.80 m s^{-1}). Water temperature in the Narsaq River increased from up- to downstream (2.6–7.4°C). Water temperature in the lake-fed tributaries NT04 and NT09 was 9.4 and 8.8°C, respectively, and was higher than that of the Narsaq River sites, but this was only marginally significant (ANOVA, $F = 5.82$, $P = 0.052$). Water chemistry data showed that all sites were low in nutrients but had circumneutral pH and were well buffered (Table 1). Conductivity ranged from 38.7 (NR01) to 62.9 μS cm^{-1} (NR07). The lake-fed tributaries had higher DOC concentrations (0.50 and 0.80 mg C L^{-1}) than that of the Narsaq River sites (0.22–0.47 mg C L^{-1}; ANOVA, $F = 7.10$, $P = 0.037$). Silica levels were between 0.78 mg L^{-1} (NR02) and 1.60 mg L^{-1} (NR07). Catchment slope ranged from 17° to 25°, mean catchment elevation from 575 to 1025 m, mean catchment NDVI from 0.16 to 0.32, and finally, catchment size from 5.17 to 36.13 km^2 (Table 2).

Biofilm characteristics

Stream biofilms were thin (< 2 mm), slimy, and golden-brown and, at times, barely visible. Chlorophyll *a* concentrations ranged from 0.008 to 0.717 μg cm^{-2} (spectrophotometer; Supporting Information Table S2) and were higher in the tributaries than in the Narsaq River (Fig. 2; Table 3, ANOVA, $F = 5.56$, $P = 0.028$). Biofilm AFDW ranged from 0.085 to 3.70 mg cm^{-2} (Fig. 2b; Supporting Information Table S2), while the autotrophic index ranged from 188 to 71,724 (Fig. 2c; Supporting Information Table S2). At every stream site, except for NT09, the index always exceeded 200, meaning that the biofilm contains large amounts of non-algal and/or non-living organic material. C : N ratio was between 4.22 and 10.38 (Fig. 2d; Supporting Information Table S2) and was greater in the tributaries (ANOVA, $F = 5.01$, $P = 0.036$; Table 3).

Autotrophic community composition

At the stream sites, the autotrophic community consisted of cyanobacteria, diatoms, and green algae (Fig. 3). Diatoms made up the majority of autotrophic biomass at the Narsaq River sites (Fig. 3a,b). At NT04, one of the lake-fed tributaries, Chl *a* concentrations of diatoms and green algae are both around 0.1 μg cm^{-2} corresponding to a relative abundance of 42%; and at NT09, the other tributary, cyanobacteria made up the majority of autotrophic biomass (75%). Total Chl *a* concentrations ranged from 0.015 to 0.31 μg cm^{-2} (Fig. 3a). Common diatom taxa in the stream biofilm were *Hannaea arcus*, *T. flocculosa*, cf. *Melosira*, cf. *Meridion*, and several other diatom spp. Common green algae genera were *Zygnema*, *Mougeotia*, *Bulbochaete*, *Cosmarium*, and *Actinotaenium*. Finally, some common cyanobacteria genera were *Nostoc*, *Komvophoron*, *Pseudanabaena*, and other Oscillatoriales.

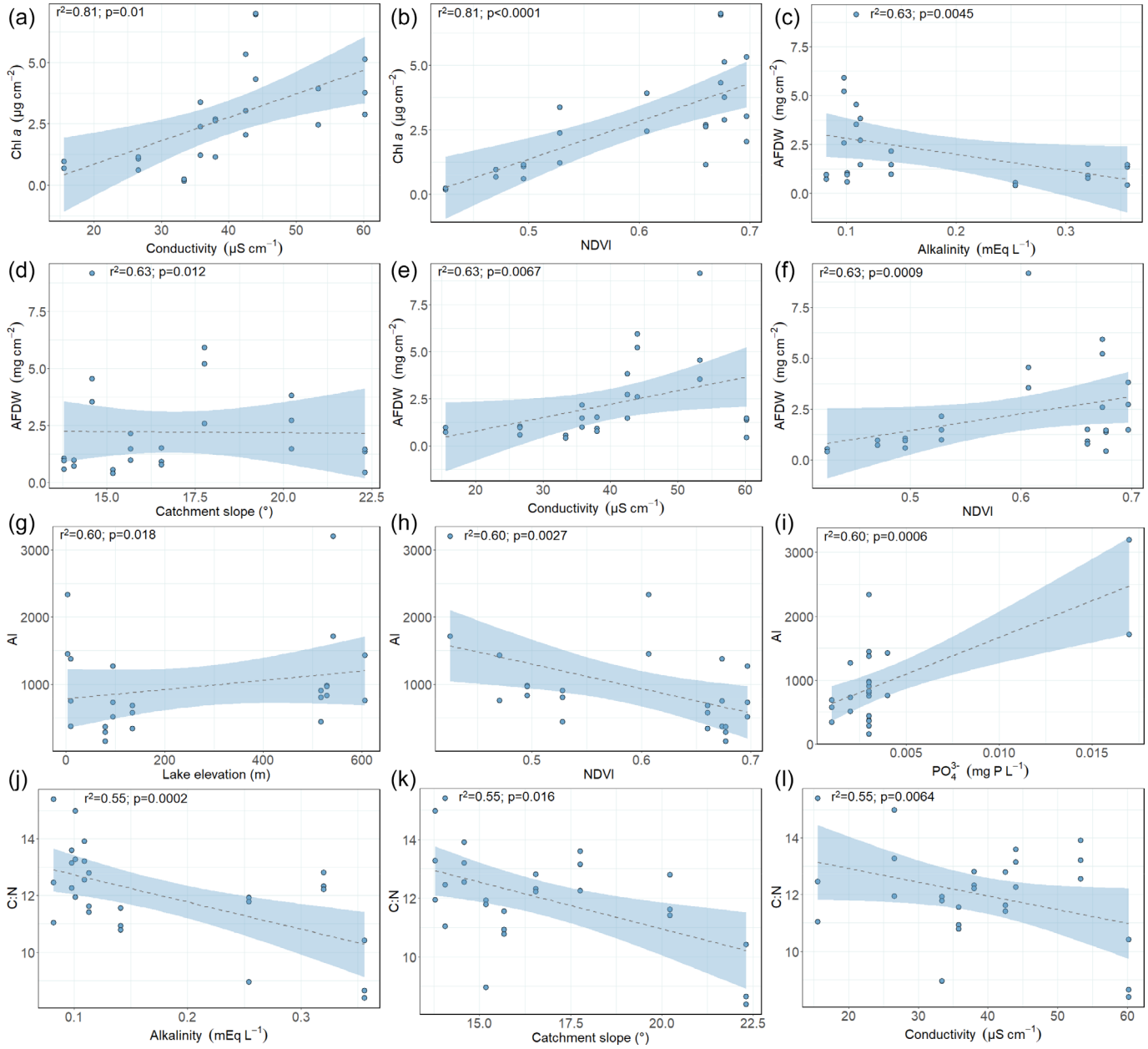

Fig. 4. Relationship between lake biofilm Chl *a* (μg cm^{-2}, spectrophotometer) and (**a**) conductivity (μS cm^{-1}), and (**b**) catchment NDVI. Relationship between lake biofilm AFDW (mg cm^{-2}) and (**c**) alkalinity (mEq L^{-1}), (**d**) catchment slope (°), (**e**) conductivity (μS cm^{-1}), and (**f**) catchment NDVI. Relationship between lake biofilm AI and (**g**) lake elevation (m), (**h**) NDVI, and (**i**) phosphate (m P L^{-1}). Relationship between lake biofilm C : N and (**j**) alkalinity (mEq L^{-1}), (**k**) catchment slope (°), and (**l**) conductivity (μS cm^{-1}). Dashed lines and light blue confidence intervals (95%) show significant regression models.

Drivers of stream epilithic biofilm biomass

Biofilm Chl *a* concentrations in the streams were related to pH ($F = 14.01$, $p = 0.0028$; Table 5; Fig. 5a), phosphate ($F = 11.01$, $p = 0.0061$; Fig. 5b), and water temperature ($F = 7.80$, $p = 0.016$; Fig. 5c). There were no significant models for AFDW, autotrophic index, and C : N ratio (Table 5). The correlation analysis among the explanatory variables showed that catchment slope was strongly correlated to water temperature (−0.93; Supporting Information Table S4), water alkalinity (−0.84), conductivity (−0.81), and silica concentrations (−0.79). In addition, catchment NDVI was strongly correlated with catchment area (0.86) and phosphate concentrations (0.82). Furthermore, water conductivity was correlated with ammonium (0.87) and silica concentrations (0.86) and alkalinity (0.83). For more correlations, *see* Supporting Information Table S4.

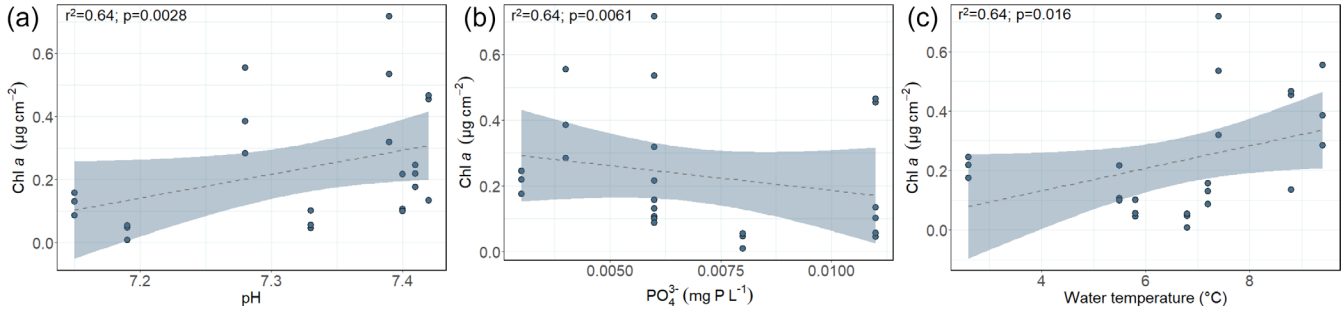

Fig. 5. Relationship between biofilm Chl *a* (μg cm^{-2}, spectrophotometer) and (**a**) pH, (**b**) phosphate (mg P L^{-1}), and (**c**) water temperature (°C) at the Narsaq River sites. Dashed lines and dark blue confidence intervals (95%) show significant regressions.

Table 5. Multiple linear regression models relating biofilm characteristics in streams to physico-chemical, catchment, and environmental variables. Data from all stream sites are included ($n = 8$). Df = 12 for all. Chl *a* is from spectrophotometer measurements.

		Estimate	*t*-value	*F* value	*p* value	Adj. R^2	Model sign.
Chl *a*	Conductivity	0.01	1.27	2.15	0.17	0.64	0.0027
	pH	1.18	1.58	14.01	0.0028**		
	PO_4^{3-}	−37.75	−2.81	11.01	0.0061**		
	Velocity	−0.18	−0.50	0.25	0.62		
	Water temperature	0.03	0.85	7.80	0.016*		
AFDW		No significant model					
AI		No significant model					
C : N		No significant model					

*$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Discussion

Despite their high sensitivity to environmental change, the relative importance of factors regulating epilithic biofilms in high-altitude and high-latitude freshwater ecosystems remains poorly understood (Battin et al. 2016; Myrstener et al. 2022; Moedt et al. 2025). This study investigated how environmental factors shape epilithic biofilm biomass and community composition in lakes and streams in subarctic Greenland. Based on previous research, we hypothesized that (1) elevation, (2) catchment characteristics (slope and greenness), (3) nutrient concentrations, and (4) habitat type would be the most important drivers of autotrophic biofilm biomass and composition in the subarctic lakes and streams. Our results supported these expectations for lakes but showed more complex or weaker patterns in streams. In lakes, biofilm biomass was positively associated with catchment greenness and water conductivity, while in streams, phosphate and temperature were key drivers. These findings align with previous work showing the importance of catchment-derived nutrients and hydrological context in Arctic freshwater systems (Vincent et al. 2012; Pastor et al. 2021; Myrstener et al. 2022). What follows is a closer examination of the key patterns observed in our study.

As expected, lake biofilm biomass decreased with elevation, consistent with findings from Finnish Lapland (Heikkinen et al. 2023) and broader Arctic and alpine patterns (Rautio et al. 2011; Clow 2010). This likely reflects shorter ice-free seasons, colder temperatures, and lower nutrient availability at higher elevations (Christianson et al. 2019). In contrast, no elevation effect was observed in streams. This may be due to varying water sources (e.g., glacial vs. lake-fed), which can mask the elevational gradients by influencing water chemistry and nutrient supply (Blaen et al. 2014a; Pastor et al. 2020; Skovsholt et al. 2020).

Catchment greenness was a strong predictor of lake biofilm biomass, likely reflecting its indirect influence via nutrient inputs and organic matter delivery (Vincent et al. 2012; Calizza et al. 2022). Both Chl *a* and AFDW were associated with greenness and slope, suggesting that vegetated, steeper catchments enhance nutrient runoff (Hogan et al. 2014; Myrstener et al. 2022; Harms et al. 2016; Riis et al. 2023). In contrast, greenness and slope were not associated with biofilm characteristics in streams, which may be due to stronger hydrological control or buffering effects in lotic environments. The observed negative correlation between phosphate and epilithic biofilm biomass in streams suggests potential co-limitation or complex nutrient interactions (Zgrundo et al. 2017; McGowan et al. 2018), possibly driven by interstitial rather than water column chemistry (Tsuchiya et al. 2016).

Phosphate and temperature were the primary predictors of biofilm biomass in streams, consistent with studies linking these factors to biofilm production (Gislason et al. 2000; Blaen

et al. 2014b; Moedt et al. 2025). While pH was also associated with biofilm biomass, the narrow circumneutral range suggests it may act as a proxy for other environmental gradients, such as nitrate availability (Harms et al. 2016; Connolly et al. 2018), as it was correlated with catchment slope. No consistent drivers of AFDW were found in streams, likely due to its relative uniformity across sites.

Stream current velocity did not influence biofilm biomass across the study streams, despite evidence from other regions showing negative effects at high flow (Rott et al. 2006; Lange et al. 2016; Fell et al. 2018). For example, filamentous algae, which are loosely attached to a substrate, are better at colonizing a streambed substrate at low current velocity (Fell et al. 2018). This lack of correlation may be due to limited variability in flow velocity among sampled sites (0.6–0.8 m s^{-1}), apart from tributary NT09 (0.16 m s^{-1}). In other systems, thinner biofilms are often observed at higher velocities due to increased shear stress, but the relationship can be modulated by other factors such as substrate type, nutrient availability, or biological controls (Hillebrand 2002; Vadeboncoeur et al. 2006; Hofmann et al. 2020; Zhao et al. 2022). For instance, top-down regulation by grazers may have masked any velocity effect by maintaining biofilm biomass at a relatively uniform level across sites.

Cyanobacteria dominated lake biofilms, as expected and consistent with other Arctic lentic systems (Quesada et al. 2008; Rautio et al. 2011; Lionard et al. 2012; Vigneron et al. 2018). In streams, biofilms included more diatoms and green algae, although cyanobacteria were also present, likely due to nitrogen limitation indicated by high N : P ratios and the presence of heterocystous taxa (Gettel et al. 2013; Quesada et al. 2008). This lentic–lotic contrast in dominant autotrophs is generally also present in temperate regions (Lange et al. 2016; Vadeboncoeur and Power 2017; Zhao et al. 2022). Similar environmental drivers, such as flow regime, light availability, and nutrient dynamics, appear to shape these communities across latitudes (Battin et al. 2003; Vadeboncoeur and Power 2017), though Arctic systems may be further influenced by stronger seasonality and nutrient limitation (Quesada et al. 2008).

Conclusion

Our results show that epilithic biofilms in lakes and streams in subarctic Greenland exhibit clear differences in biomass and autotrophic composition, shaped by distinct environmental drivers reflecting differences in hydrological connectivity and internal ecosystem dynamics. Lake biofilm biomass was primarily linked to catchment greenness and water conductivity, emphasizing the significant role of external nutrient and organic matter inputs transported from the surrounding landscape. In contrast, stream biofilms responded more strongly to internal factors such as water temperature, indicating tighter control by local hydrology and in-stream processes. The autotrophic communities also followed this lentic–lotic divide, with cyanobacteria dominating lake biofilms and diatoms and green algae more prevalent in streams, a pattern consistent with studies from both Arctic and temperate regions. These contrasting controls highlight the need to consider habitat-specific drivers when predicting biofilm responses to climate-driven environmental change. By linking key environmental variables to biofilm biomass and community composition, our study not only advances understanding of Arctic freshwater ecosystem sensitivity but also establishes an important regional baseline for South Greenland. The patterns revealed here have broader implications for forecasting how biofilms, and the ecosystem functions they support, may shift across high-latitude freshwater systems under ongoing climate warming.

Author Contributions

Sanne Mariël Moedt: Conceptualization (equal); investigation (equal); formal analysis (lead); writing—original draft (lead); writing—review and editing (equal). Tenna Riis: Conceptualization (equal); investigation (equal); formal analysis (supporting); writing—original draft (supporting); writing—review and editing (equal). Dean Jacobsen: Investigation (equal); writing—review and editing (equal). Ole Geertz-Hansen: Investigation (equal); writing—review and editing (equal). Kenneth Thorø Martinsen: Formal analysis (supporting); writing—review and editing (equal). Kirsten Seestern Christoffersen: Conceptualization (equal); investigation (equal); formal analysis (supporting); writing—original draft (supporting); writing—review and editing (equal).

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Conflicts of Interest

None declared.

Data Availability Statement

Environmental and biofilm data are available at PANGAEA, https://doi.pangaea.de/10.1594/PANGAEA.974506 (dataset in review). The Sentinel-2 Level-2A product used in this study (ID: S2B_MSIL2A_20220822T143749_N0400_R039_T23VMH_20220822T172435) is available from the Copernicus Open Access Hub (https://scihub.copernicus.eu/) under the European Union's Copernicus program.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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