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Epilithic Algal and Meiofaunal Assemblages of Arctic/Alpine Lakes and Streams Along Latitudinal and Environmental Gradients in Scandinavia

Willem Goedkoop[1] | Sebastian Höss[2] | Fernando Chaguaceda[1,3] | Kirsten S. Christoffersen[4] | Walter Traunspurger[5]

[1]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden | [2]Ecossa (Ecological Sediment and Soil Assessment), Starnberg, Germany | [3]IMDEA Water, Madrid, Spain | [4]Freshwater Biological Laboratory, Department of Biology, University of Copenhagen, Copenhagen, Denmark | [5]Department of Animal Ecology, Bielefeld University, Bielefeld, Germany

Correspondence: Willem Goedkoop (willem.goedkoop@slu.se)

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ABSTRACT

1. Epilithic biofilms along a latitudinal gradient of Arctic/alpine lakes and streams were analysed for their composition of algae (incl. cyanobacteria) and meiofaunal assemblages and correlated these with environmental variables.
2. The composition of algal, meiofauna and nematode assemblages differed between lakes and streams. Algal biovolumes were higher for lakes ($373–6456\,\mathrm{mm}^3/10\,\mathrm{cm}^2$) than for streams ($7.1–8763\,\mathrm{mm}^3/10\,\mathrm{cm}^2$), as were their carbon concentrations (32.9–393 and 10.7–211 mgC/gDW, respectively). Stream assemblages were frequently predominated by green algae, that is, $>48\%$ of total biovolume, whereas lakes were predominated by diatoms ($n=3$ lakes) or cyanobacteria ($n=8$ lakes).
3. Meiofauna biomass averaged $486 \pm 90.3\,\mu\mathrm{gDW}/10\,\mathrm{cm}^2$ for lakes and $262 \pm 94.2\,\mu\mathrm{gDW}/10\,\mathrm{cm}^2$ for streams and was numerically predominated by nematodes, followed by rotifers. Harpacticoid copepods and cladocerans, largely absent in streams, were most abundant in lakes. Nematode species richness ranged 7–25 for lakes and 3–20 for streams and showed a strong predominance of bacteria-feeders ($>80\%$).
4. Algal assemblages did not correlate with environmental variables, but lakes split into two distinct subgroups, separated by nutrients and TOC. Abundances of cladocerans, nematodes and cyclopoids correlated with nutrient concentrations and TOC, while nematode composition also correlated with N, Cl and with diatom biovolume.
5. Estimates of meiofauna biomass were similar to or exceeded those of epilimnetic zooplankton, while the biovolume of benthic algae was more than 1000× higher than that of epilimnetic phytoplankton in similar lakes. Combining these patterns emphasises the importance and complexity of the epilithic biofilm habitat and its role in lake food webs.
6. Our study revealed biofilm assemblages of lakes and streams are highly diverse and distinctly different. This unique dataset provides insight into the limited latitudinal changes in meiofauna assemblages of northern lakes and streams and establishes a baseline to gauge the effects of future climate-induced change.

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1 | Introduction

Arctic and northern regions experience rates of climate warming that are more than twice as high as the global average (IPCC 2014; Rantanen et al. 2022). For example, even IPCC's moderately conservative RCP4.5 scenario predicts a 2.5°C–3.5°C warmer climate in Northern Scandinavia by the year 2100. Ongoing warming results in the melting of glaciers (AMAP 2021), the thawing of permafrost (Kokelj et al. 2013; AMAP 2021), as well as the gradual greening of tundra landscapes (Pouliot et al. 2009; Jenkins et al. 2020) and concurrent transformation into shrublands (Elmendorf et al. 2012). These gradual, large-scale landscape transformations also impact the quality of surface water run-off and the biodiversity of lakes and rivers (Lento et al. 2019; Heino et al. 2020). In response to warming, cold-adapted species are expected to shift their range to higher latitudes or elevations (IPCC 2014; Goedkoop et al. 2022). The ongoing change in water quality (Huser et al. 2022) and its effects on freshwater biodiversity are partly covered by national monitoring programmes and ideally reported to transnational organisations such as the European Union, GEO-BON (The Biodiversity Observation Network of the Group of Earth Observations) or CAFF (Conservation of Arctic Flora and Fauna) to provide larger-scale assessments (e.g., European Environment Agency 2018; Lento et al. 2019). Freshwater biomonitoring has traditionally covered biological variables such as plankton, epilithic algae, macroinvertebrates and fish, but has largely neglected the smaller fauna of biofilms and sediments (but see Höss et al. 2011; Bighiu et al. 2020).

Biofilms cover almost all submersed surfaces and are complex assemblages of algae, microbes, protozoan microfauna and meiofauna, embedded in a matrix of extracellular polymeric substances (Romani Cornet et al. 2016; Battin et al. 2016; Weitere et al. 2018). Biofilms are sites of high biological activity and play key roles in ecosystems (Hakenkamp and Morin 2000), such as the trophic upgrading of detritus (Werbrouck et al. 2017; Weitere et al. 2018) and the transfer of basal resources to invertebrate consumers and fish (Vadeboncoeur and Power 2017; Peters et al. 2012). Indeed, benthic trophic pathways are frequently underestimated as scientists tend to have an overly strong focus on pelagic trophic pathways (VanderZanden and Vadeboncoeur 2002), while these in fact play a minor role in food web processes of nutrient-poor, clearwater lakes and streams (Vadeboncoeur et al. 2003). Multiple studies have shown high abundances of small fauna in freshwater biofilms (Peters and Traunspurger 2005; Schroeder, Peters, and Traunspurger 2012; Schroeder, Traunspurger, et al. 2012) and surface sediments (Goedkoop and Johnson 1996; Ristau and Traunspurger 2011; Traunspurger et al. 2012). Total annual secondary production by meiofauna in four investigated microhabitats of the Furlbach (Germany) was 2.3 g C/m^2, with organisms in sediment contributing 48%, and those on dead wood 43%, respectively (Brüchner-Hüttemann et al. 2020). Similarly, Goedkoop and Johnson (1996) showed that lake sediment meiofauna and chironomid macrofauna assimilated and respired similar proportions of a settling diatom spring bloom. Indeed, despite their small size and low biomass compared to macrofauna (e.g., Strayer 1985; Nalepa and Quigley 1983), the relatively high metabolic rates of meiofauna (e.g., Banse 1982) may significantly contribute to ecosystem processes (Goedkoop and Johnson 1996; Majdi et al. 2017). However, their small size also complicates the study of meiofauna, which likely has contributed to their limited role in ecological studies and conservation biodiversity.

Biofilm primary producers in northern streams (Myrstener et al. 2017) and lakes (Liess et al. 2009; Diehl et al. 2018) are frequently nitrogen-limited, usually resulting in a predominance of nitrogen-fixing cyanobacteria. Benthic primary producers are the base of food webs in clearwater lakes and streams with strong trophic links to invertebrates and fish that feed in these habitats (Vadeboncoeur and Power 2017). However, the community composition of algae is of key importance for the trophic transfer efficiency of nutrients and energy to consumers (Brett and Müller-Navarra 1997; Ravet et al. 2003; Goedkoop et al. 2007). In trophic ecology, diatoms are generally considered high-quality food as they are rich in long-chain poly-unsaturated fatty acids (LC-PUFA) that support high growth rates and are key for maturation and development of invertebrate grazers. Conversely, cyanobacteria are deprived of these LC-PUFA and are considered a low-quality food resource for consumers (Brett and Müller-Navarra 1997). Knowledge of the composition of benthic biofilm assemblages therefore provides important information about the basal food resources (and their quality), and the trophic transfer efficiency across the plant-invertebrate interface. Despite their key importance as basal resources, little is known about the composition and sensitivity of benthic biofilms to climate warming, especially so in high-latitude and high-elevation ecosystems (Wang et al. 2022; Moedt et al. 2025).

Stream communities experience a unidirectional flow and are primarily controlled by stochastic floods (Resh et al. 1988; Lake 2000), causing mobilisation of the streambed and abrasion of attached biofilms (Graba et al. 2014) and invertebrates (Lepori and Hjerdt 2006). Similarly, bottom-freezing in streams occurs regularly in the cold regions (see Tolonen et al. 2019 for review) and severely impacts biofilm assemblages. Conversely, lake littoral habitats are subjected to multidirectional water currents, are hydrologically more stable (less shear stress), and provide proximate refugia in sublittoral habitats under the ice. Both lake and stream biofilm habitats and their associated communities will likely adapt to climate warming through gradual species replacements and a loss of cold-adapted species (Goedkoop et al. 2022). For example, cyanobacteria are expected to benefit from warmer conditions (Schartau et al. 2022), but so far little is known about the responses of Arctic/subarctic meiofaunal communities to climate warming, although some valuable baseline data exist (Walseng et al. 2018).

In this study we assess compositional changes in primary producers and meiofauna in epilithic biofilms along a latitudinal gradient of remote, clearwater lakes and streams in subarctic Sweden. In addition to climate variables, we have measured a set of environmental variables to study how these relate to compositional changes in meiofauna and algal assemblages, as well as nematode communities, changing across latitudinal (climatic) and environmental gradients. We hypothesised (1) that the biovolume of cyanobacteria among benthic primary producers would increase and (2) that the biomass of meiofauna would decrease across the south–north gradient. Further, we expected (3) compositional changes of nematode communities across the north–south gradient and (4) that microcrustaceans would show higher densities in lakes than in streams, due to the difference in disturbance regime between the two habitats, as lake biofilms are more stable and well developed, which allows them to alternate their feeding in both benthic and pelagic habitats. Our study is the first to assess community compositional changes of both meiofauna and algae across a latitudinal gradient for multiple remote lakes and streams in the earth's cold regions.

2 | Materials and Methods

2.1 | Study Sites

The lakes and streams in this study are all situated in the Arctic/alpine ecoregion of Sweden (Nordic Council of Ministers 1984; Gustafsson and Ahlén 1996), a remote and relatively undisturbed ecoregion along the Scandes Mountain range that traverses the Arctic circle in northern Scandinavia. The Artic/alpine ecoregion combines the Arctic ecoregion (i.e., north of the Arctic circle) with the alpine ecoregion (alpine tundra landscape south of the Arctic circle) to give the Arctic/alpine complex. The ecoregion is characterised by mean annual temperature ranges from 0°C in the south to −3°C in the north, but is subjected to gradual warming and greening (Elmendorf et al. 2012; Kullman 2021). Mean degree-days for 2016–2020 for the summer months (June–September) ranged from 209° for the northernmost lake (L11) to 332° for the southernmost lake (L1). The ecoregion's vegetation cover is predominated by mountain birch, willow and sparse spruce/pine forests below the tree line (approximately 650 m in the north, 900 m in the south) and with tundra vegetation (heath, dwarf shrubs, grasses) and bare rock at higher elevations. Eleven lakes (L1–11) and nine streams (S2–10), situated at 442–936 m a.s.l. between 62.79° N and 68.43° (i.e., corresponding to a south–north gradient of more than 600 km), were sampled in the summer (July/August) of 2021 (Figure 1). These water bodies were all highly oligotrophic, clear-water ecosystems (Total-P $< 5\,\mu$g/L), with ice-out commonly occurring between late May in the northern and mid-June in the southern end of the gradient. Selected morphometric and biogeochemical characteristics of the study sites are listed in Table S1. The sites were reached either by car, helicopter and/or hikes.

2.2 | Field Work

Surface water samples were collected approximately 6–8 m out from the shoreline in lakes and in midstream using an adjustable rod and plastic bottles and sent in cooling packs on the same day by mail to SLU's accredited (Swedish Board for Accreditation and Conformity Assessment, SWEDAC) laboratory for analyses. These samples usually arrived the day after and were analysed for a set of standard water chemistry variables (see below).

Quantitative meiofauna samples ($n = 5$) were collected from five cobble-size rocks at different locations (between 0.5 and 1 m depth) in the littoral zone of lakes or across the stream channel using a cylindrical brush sampler with a surface area of 3.14 cm^2 (Peters et al. 2005). The sampler was placed under water on a flat part of the upper surface of the rock and brushed for 30 s. The sample was then transferred to 50-mL plastic tubes and preserved with formaldehyde (final concentration 4%).

Epilithic algae samples ($n = 5$) were also collected from five cobble-size rocks at different locations in the littoral zone (lakes) or across the stream channel using the under-water brush sampler described above (Peters et al. 2005). These samples were transferred to 50-mL plastic tubes and fixed with Lugol's solution for later analyses of algal communities. Epilithic samples for stable isotope analysis were sampled by brushing an additional five rocks with a toothbrush and washing the material into a tray with a small volume of lake water. Macroinvertebrates and plant remains were removed with forceps and the slurry was transferred to 250-mL polyethylene flasks to form a single sample. These samples were then frozen in the field (when liquid nitrogen or dry ice was available) or kept cool and dark (cooling blocks) and placed in a freezer at the end of the day. Pictures of the five cobbles were taken from a 90-degree angle for later calculation of their water-exposed surface using an image analysis application.

2.3 | Laboratory Work

Water chemistry analyses followed Swedish or European standards standard protocols in our accredited laboratory and included inorganic nutrients, alkalinity, pH, major ions, TOC, water colour and conductivity. Detailed descriptions of methods, detection limits and quality control can be found at https://www.slu.se/en/departments/aquatic-sciences-assessment/laboratories/vattenlabb2/.

Meiofauna samples were processed using density centrifugation techniques with Ludox-TM50 (silica suspension, 1.13 g/mL) according to Pfannkuche and Thiel (1988). The extraction procedure was repeated two times (three extractions in total) and the supernatant with meiobenthic organisms was sieved through a net (mesh size 10 μm) and stained with Bengal Rose (300 μg/mL). Meiobenthos organism groups, that is, Nematoda, Rotatoria, Copepoda (harpacticoid, cyclopoid), Cladocera, Ostracoda, Oligochaeta, Chironomidae, Acari, Gastrotricha and Tardigrada, were sorted and counted under a stereomicroscope (40-fold magnification). If present, 100 randomly selected nematodes were mounted for species-level identification following Seinhorst (1959). Nematode species were assigned to feeding types following Traunspurger (1997): Bacteria-feeders (deposit-feeders), algae feeders (epistrate feeders), suction feeders (plant/root/fungi feeders), omnivores (incl. omnivorous suction feeders and chewers) and predators. In total, 4543 nematodes were identified from lake samples and 2294 from stream samples. Due to the low nematode density (< 10) in some replicates, data from 5 replicates were pooled (summed) for the calculation of relative species densities.

Biomass of nematodes was calculated following Andrássy (1956) and using own measurements of adults and juvenile stages of each nematode species. Densities of oligochaetes, harpacticoid copepods and ostracods were converted into biomass (dry weight) using the estimates by Faubel (1982) (Table 1). The specific gravity was assumed to be 1.13 g/cm^3, the dry/wet weight ratio 0.25, and the C content/dry weight ratio 0.45 (Feller and Warwick 1988). When these did not match our taxa (i.e., for Tardigrada, Gastrotrichia and Ostracoda), conservative values were extracted from table 2 in Faubel (1982). Dry weight

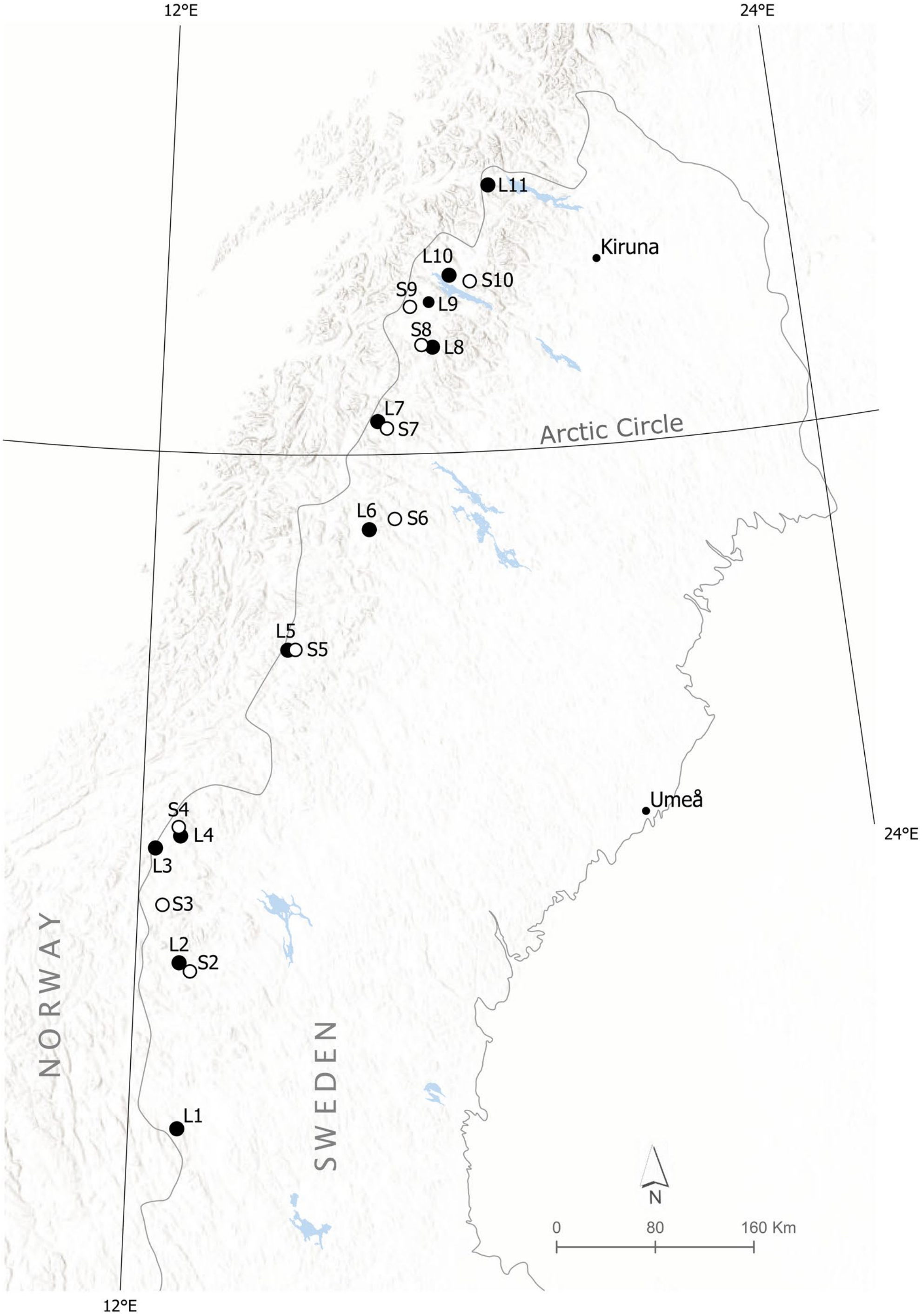

FIGURE 1 | Map of northern Scandinavia showing the locations of the study lakes (black) and streams (white) in the Scandes. Notations correspond to those used in Table S1, where details of the lakes and streams are given. Two longitude meridians and the Arctic circle (appr. 66.55°N) are shown to facilitate global orientation.

biomass estimates for other microcrustaceans were taken from Nauwerck (1963, table 12), while biomass of Rotatoria was calculated using a median volume from Nauwerck (1963) and the relationship between volume and dry weight biomass for *Brachionus plicatilis* by Theilacker and Kimball (1984, table 4). Biomass of early instar chironomids was calculated using a length-dry weight relationship for *Chironomus* sp. (Reyes-Maldonado et al. 2021) and assuming first instar larvae were 0.20 mm long.

Taxonomic identification of epilithic algae (incl. cyanobacteria) was done on four of five subsamples. The slurries were shaken well, if necessary homogenised with forceps, and diluted to concentrations appropriate for counting. Samples were then transferred to a 2.1-mL Utermöhl counting chamber and analysed using an inverted microscope (Olympus-IMT2). Small and medium-sized cells were counted in half of the chamber at 400× and 200× magnification, respectively, while larger cells were counted along half the diagonal at 100× magnification. Only living cells were

TABLE 1 | Biomass (μgDW/10 cm^2) of different groups of meiofauna in epilithic biofilms of lakes (L) and streams (S). Numbers represent means (±1 SE) for 5 replicate samples.

Site code	Harpac-ticoida	Cladocera	Ostracoda	Chirono-midae	Nematoda	Oligochaeta	Rotatoria	Tardigrada	Gastro-tricha	Sum
L1	0.4 ± 0.4	30 ± 13	0	8.1 ± 5.0	2.7 ± 8.9	0	3.5 ± 1.1	0	0	48
L2	76 ± 9.1	83 ± 6.2	0	114 ± 35	85 ± 27	63 ± 25	13 ± 1.4	0	0	435
L3	30 ± 4.4	60 ± 9.8	0	102 ± 32	133 ± 29	229 ± 70	12 ± 2.3	0.6 ± 0.6	1.8 ± 1.8	569
L4	14 ± 5.8	115 ± 21	0	94 ± 46	127 ± 19	200 ± 87	12 ± 2.5	0	13 ± 7.8	587
L5	79 ± 18	132 ± 25	0	188 ± 44	406 ± 75	63 ± 16	45 ± 6.9	13 ± 4.5	1.8 ± 1.8	943
L6	44 ± 13	136 ± 52	0	98 ± 30	228 ± 37	478 ± 189	17 ± 3.3	6.4 ± 2.8	1.8 ± 1.8	1013
L7	12 ± 3.8	11 ± 6.6	0	65 ± 20	47 ± 27	28 ± 16	1.9 ± 0.7	1.0 ± 0.4	0	166
L8	22 ± 16	17 ± 9.2	0	70 ± 26	64 ± 32	3.5 ± 3.5	5.7 ± 2.0	2.2 ± 1.4	0	184
L9	48 ± 11	59 ± 13	15 ± 10	90 ± 12	162 ± 61	39 ± 18	9.8 ± 3.6	0	11 ± 11	451
L10	1.8 ± 0.8	0	0	278 ± 96	116 ± 28	0	14 ± 8.8	20 ± 16	0.4 ± 0.4	431
L11	12 ± 2.2	102 ± 25	0	290 ± 33	65 ± 16	11 ± 7.0	6.6 ± 1.4	3.2 ± 2.0	0	521
Overall mean	30.8 ± 8.3	67.8 ± 14.9	1.4 ± 1.4	127 ± 27	131 ± 33	101 ± 45	12.7 ± 3.5	4.2 ± 2.0	2.7 ± 1.4	486 ± 90
S2	0	0	15 ± 6.1	20 ± 9.1	2.7 ± 11	7.0 ± 7.0	2.5 ± 1.2	1.6 ± 1.0	1.3 ± 0.9	52
S3	1.8 ± 1.8	0	5.0 ± 5.0	20 ± 9.1	1.1 ± 0.9	0	0.9 ± 0.2	4.1 ± 1.9	0	33
S4	1.1 ± 0.7	0	0	53 ± 24	96 ± 51	14 ± 6.6	13 ± 5.3	2.6 ± 0.8	0	180
S5	0.4 ± 0.4	0	0	45 ± 15	3.8 ± 6.0	14 ± 14	1.3 ± 0.7	1.6 ± 1.2	0	66
S6	1.4 ± 1.0	0	5.0 ± 5.0	114 ± 8.2	100 ± 51	14 ± 6.6	38 ± 7.1	8.3 ± 1.9	0	281
S7	5.7 ± 2.2	1.4 ± 1.4	5.0 ± 5.0	254 ± 94	57 ± 29	14 ± 10	25 ± 6.2	37 ± 12	0	399
S8	2.5 ± 2.0	1.4 ± 1.4	0	49 ± 30	8.9 ± 4.4	25 ± 13	3.6 ± 1.5	15 ± 4.8	0.4 ± 0.4	105
S9	11 ± 8.7	7.2 ± 2.3	50 ± 39	793 ± 123	33 ± 27	11 ± 7.0	6.6 ± 1.6	18 ± 12	3.6 ± 3.6	934
S10	13 ± 2.3	60 ± 16	0	155 ± 29	11 ± 37	42 ± 19	8.7 ± 2.0	9.2 ± 3.0	0	307
Overall mean	4.1 ± 1.6	7.8 ± 6.6	8.9 ± 5.4	167 ± 82	34.8 ± 13.4	15.7 ± 4.0	11.1 ± 4.2	10.8 ± 3.8	0.6 ± 0.4	262 ± 94

counted. Species that occurred with five or more individuals were included in biovolume calculations. Biovolume was estimated by fitting the algae (and cyanobacteria) to the appropriate geometrical shapes and measuring the dimensions of 10 individuals per taxon (Hillebrand et al. 1999). Hidden dimensions were estimated according to European Standards (EN 16695 2015). Results are presented as biovolume ($mm^3/10\,cm^2$) or as percent of the total epilithic sample biovolume. We refer to benthic algae in this manuscript, which includes both algae and cyanobacteria.

Temperature data for each of the sites was extracted from Climatic Research Unit gridded Time Series (CRU TS) database, version 4.06 (Harris et al. 2020). Mean daily temperatures for July–September were used to calculate ∑degreedays which provided a better climatic gradient than latitude, as it also corrects for differences in elevation (see above).

2.4 | Statistical Analysis

Water chemistry variables that were below the limit of detection (LOD) were set at half the LOD in statistical analyses, that is, for PO_4—P (LOD 1 μg/L), for NH_4—N (LOD 3 μg/L) and for NO_2+NO_3—N (LOD 1 μg/L). Principle Component Analysis (PCA) was performed to identify gradients in water chemistry for lakes and streams using CANOCO v.4.55 (ter Braak and Šmilauer 2002). Relationships between biota community structure and environmental variables were analysed using multivariate ordination models after running detrended correspondence analysis (DCA) to assess gradient lengths. DCA gave gradient lengths >4 for our algae data set and <2.0 for the faunal data sets. Accordingly, we ran Canonical Correspondence Analysis (CCA) and partial-CCA (pCCA) to analyse algal-environmental relationships, while redundancy analysis (RDA) and partial-RDA (pRDA) were used to analyse the faunal data sets. Prior to analysis, data were arcsin-square root transformed and standardised around the mean and divided by their standard deviation. RDAs and CCA were run in R v4.3.1 (R Core Team 2023; Oksanen et al. 2022). Ordinations were run using forward selection of environmental variables, permutation *p*-values and *r*-square maximisation based on Blanchet et al. (2008) to evaluate the influence of environmental variables (i.e., water temperature, pH, alkalinity, nutrients [total phosphorus and total nitrogen, NO_2+NO_3, NH_4], TOC, and chloride, latitude, elevation, degree-days) on the mean relative abundance ($\log(x+1)$-transformed) of epilithic algae (based on biovolume), meiofauna groups and nematode species (pooled replicates), respectively. As the RDAs showed that most of the variation was explained by ecosystem type (i.e., lakes or streams), we ran partial-RDA (pRDA) with ecosystem type as a conditioning variable in order to strictly focus on effects of environmental variables. Log-transformed data were used in *t*-tests to compare single variables between lakes and streams. Relationships of algal biovolumes and meiofauna biomass with latitude were analysed using linear regressions. Alpha was set at 0.05 in all statistics.

3 | Results

Water chemistry data showed that all water bodies were ultra-oligotrophic, with total-P concentrations ranging 1.5–3.9 and 0.7–4.0 μg P/L for lakes and streams, respectively. Total-N concentrations were also low, ranging 25–145 μg N/L for lakes and 25–113 μg N/L for streams. Phosphate-P concentrations were below the LOD for all samples (i.e., <1 μg/L), while ionic nitrogen fractions had concentrations that were under the LOD (3 μg/L for NH_4-N and 1 μg/L for NO_2-N + NO_3-N) in 47% and 44% of the measurements for NH_4-N and (NO_2+NO_3)-N, respectively. All sites, except southernmost lake L1 (pH 5.7), had circumneutral pH ranging 6.3–7.9 and were well oxygenated at the time of sampling (≥ 8.7 mg O_2/L). Lake L1 also had a very low alkalinity of 0.004 meq/L, whereas for all other water bodies it ranged from 0.030 to 0.298 meq/L. TOC never exceeded 5.0 μg/L for any of the water bodies. Water chemistry data and other characteristics for all sites are given in Table S1.

PCA on water chemistry data revealed gradients in water colour, TOC and total-N towards those with higher alkalinity and higher concentrations of major cations along the first PC-axis, which explained 35.2% of the variability (Figure 2). The second axis explained another 26.2% of the variability, largely related to gradients in NO_2+NO_3-N and pH. The gradients identified by the PCA were generally narrow, which is a consequence of the fact that all lakes and streams were ultra-oligotrophic and low in TOC (Table S1).

Diatoms (Bacillariophyta), green algae (Chlorophyta) and cyanobacteria (Cyanophyta) were the most common groups among epilithic primary producer assemblages, but their biovolumes varied markedly within and among the sites (Figure 3). Lake biofilms had higher biovolumes of primary producers (*t*-test, $p=0.0205$) and of cyanobacteria alone than those of streams (*t*-test, $p<0.001$). Site L5 had an extremely high biovolume of cyanobacteria, that is, 6267 $mm^3/10\,cm^2$, while S9 was extremely rich in chlorophytes (predominantly *Mougeotia* spp.), that is, 8619 $mm^3/10\,cm^2$, respectively. Three of the lakes (L6,

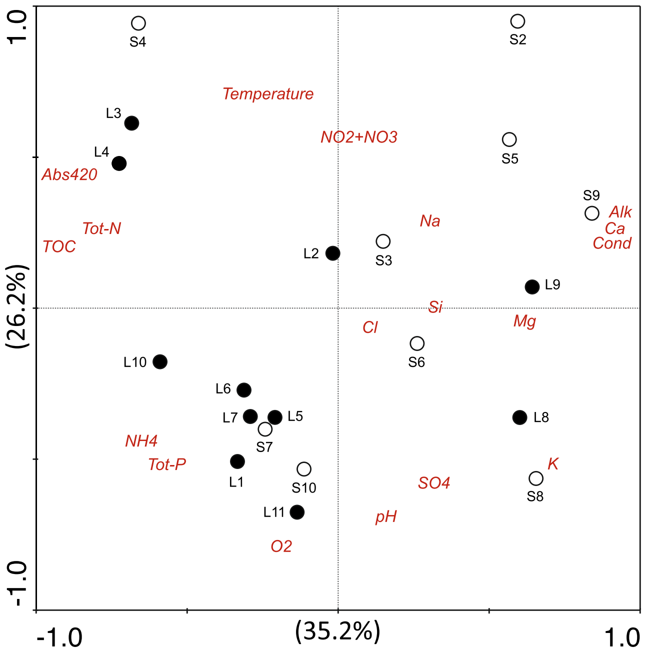

FIGURE 2 | PCA of environmental variables for lakes (black) and streams (white).

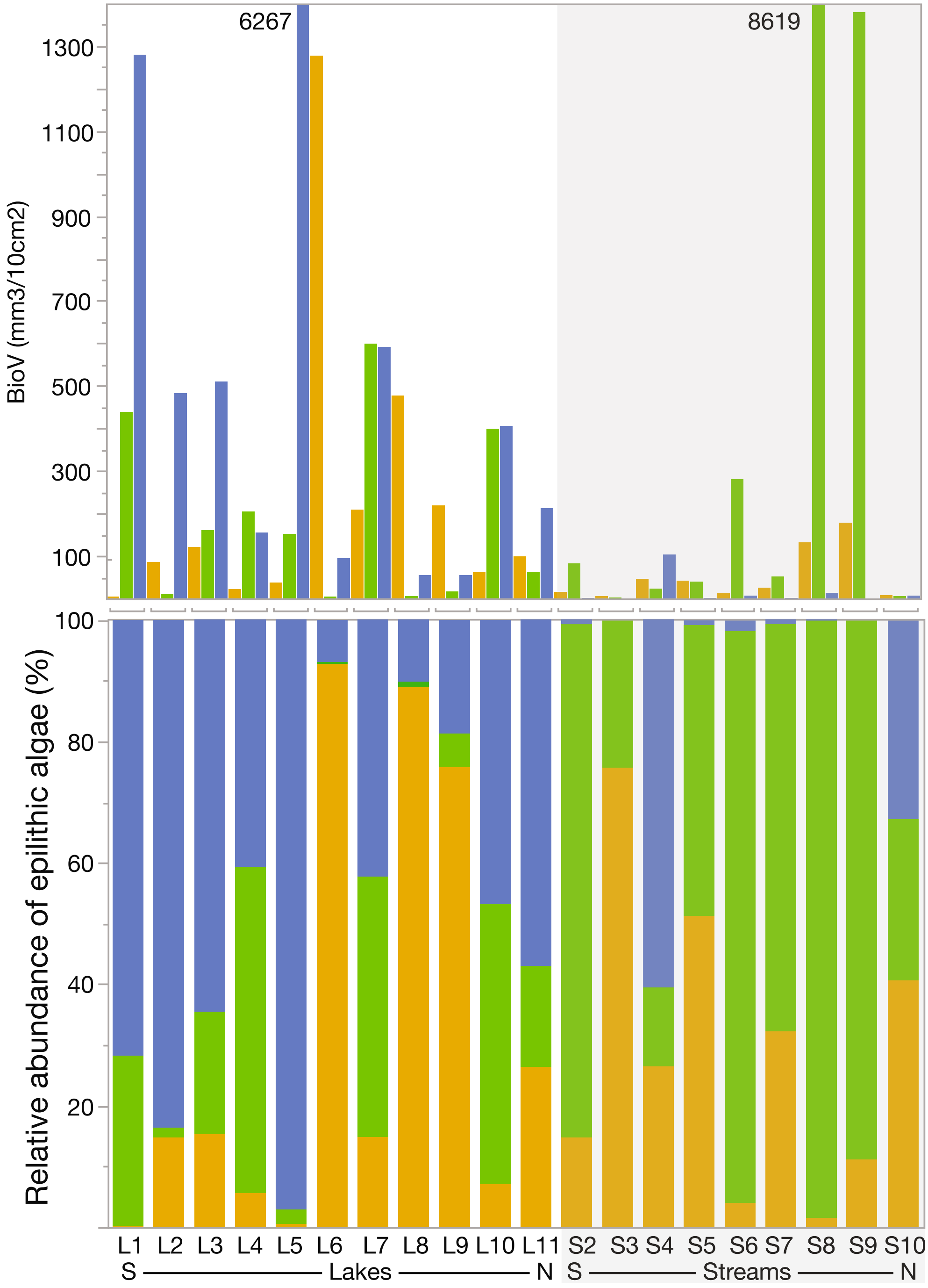

FIGURE 3 | Epilithic algal biovolume ($mm^3/10\,cm^2$) (upper) and relative abundance based on biovolume (lower) for Bacillariophyta (orange), Chlorophyta (green) and cyanobacteria (blue) for lakes and streams (shaded part) along latitudinal gradients starting from south (S) to north (N). Note that two high values that are outside of the scale in the upper panel are given by their numbers.

L8 and L9) showed a strong predominance of diatoms, making up 76%–93% (or 12.0–476 mm^3/cm^2) of total biovolume. Stream epilithic assemblages were frequently predominated by green algae, which exceeded 48% of total biovolume in five of nine streams (range 39.9–8619 $mm^3/10\,cm^2$). Streams S3 and S10 had poorly developed epilithic biofilms with algal biovolumes being $<18\,mm^3/10\,cm^2$. Overall, epilithic algal and cyanobacterial biovolumes ranged 373–6456 $mm^3/10\,cm^2$ for lakes and 7.1–8763 $mm^3/10\,cm^2$ for streams. Biovolumes of diatoms, green algae and cyanobacteria showed no relationship with latitude (linear regression, $p>0.05$, data not shown).

Carbon concentrations in biofilms were higher for lakes than for streams (*t*-test, $p=0.045$) and were on average 148.2 ± 29.6 mg/gDW (range 32.9–393) and 98.6 ± 25.5 mg/gDW (range 10.7–211). Likewise, biofilm C per surface area was higher for lakes than for streams (*t*-test, $p=0.048$), but that of N was not. Nitrogen concentrations of biofilms did not differ between lakes and streams and were on average 11.6 ± 2.5 mg/gDW (range 1.8–32.5) and 7.9 ± 1.9 mg/gDW (range 1.1–16.4), respectively. Visual observations revealed that some biofilms with low C or N concentrations were relatively rich in mineral particles, that is, fine inorganic particles trapped in the exopolymeric matrix of the biofilms

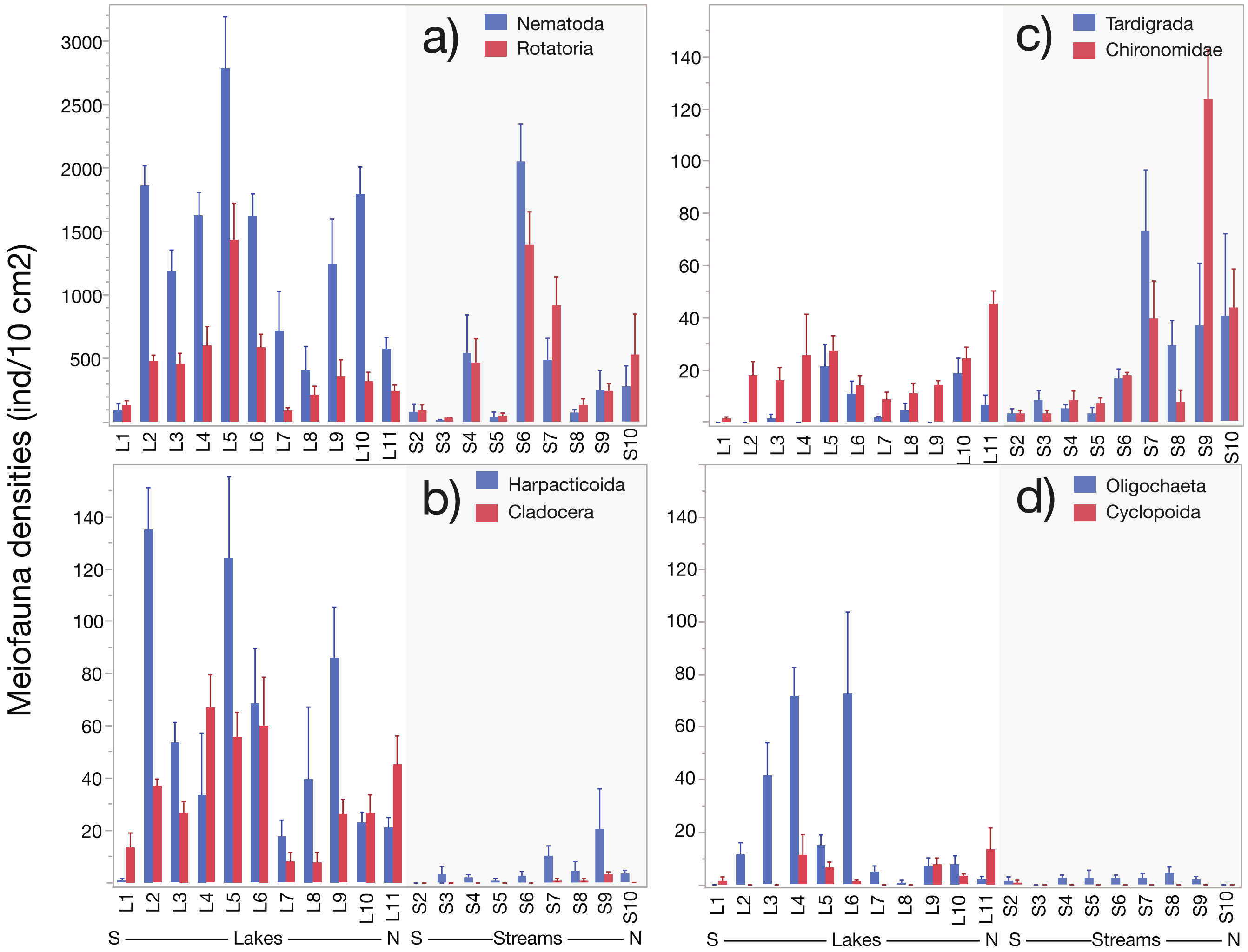

FIGURE 4 | Densities of Nematoda and Rotatoria (a), Harpacticoida and Cladocera (b), Tardigrada and Chironomidae (c), and Oligochaeta and Cyclopoida (d) in epilithic habitats of lakes (L1–L11, white background) and streams (S2–S10, shaded background). Results are given for lakes and streams along latitudinal gradients from north (N) to south (S). Error bars denote 1 standard error. Note the differences in scale between the a-panel and the other panels.

(i.e., L3, L4, L6, S5 and S6). Biofilm C per 10 cm^2 was higher for lakes than for streams (*t*-test, $p = 0.048$), but N was not (*t*-test, $p > 0.05$). Lake biofilms were higher in δ^{13}C (*t*-test, $p < 0.001$) than stream biofilms, that is, −26.7 ± 1.1 (range −30.3 to −20.7) and −0.29 ± 0.45 (range −11.1 to 3.63), respectively (Table S2). Conversely, stream biofilms were slightly higher in δ^{15}N (*t*-test, $p = 0.0331$) than lake biofilms, that is, 0.29 ± 0.45 (range −1.12 to 3.64) and −0.68 ± 0.16 (range −1.56 to 0.44), respectively.

Meiofauna was numerically predominated by nematodes in lakes and by rotifers in streams (Figure 4a; Table S3). Nematode densities among streams ranged from 11.5 ± 5.1 ind/10 cm^2 (mean ± standard error, used throughout) in S3 to 2046 ± 299 ind/10 cm^2 in S6, while that among lakes ranged from 92.4 ± 52.5 ind/10 cm^2 in L1 to 2975 ± 410 ind/10 cm^2 in L5. Nematode densities were slightly, albeit significantly, higher in lakes than in streams (*t*-test, $p = 0.021$), but the data showed high variability. Nematodes were predominantly bactivorous taxa, that is, making up 55%–98% in lakes and 58%–100% in stream biofilms (Table S4). Algae-feeders were common only in L3 and S9, where they made up 29% and 28% of the nematode fauna, respectively, but were otherwise absent or < 8% in lakes and 0.5% in streams. Nematodes classified as omnivores (chewers and suction feeders) made up 2.3% in lakes and 19.7% in streams. In total, 52 nematode species were identified in lake biofilms (range 7–25) and 38 species in stream biofilms (range 3–20). Common species (total mean relative abundance of > 5%) were the bactivorous *Eumonhystera vulgaris*, *Rhabdolaimus aquaticus*, *Plectus aquatilis*, and *Udonchus* sp. and the omnivorous *Epidorylaimus agilis* and *Mesodorylaimus* cf. *bastiani* (Table S4). Rotifer densities ranged from 47 ± 26 ind/10 cm^2 in S5 to 1636 ± 254 ind/10 cm^2 in L5 and were similar for lakes and streams (*t*-test, $p > 0.05$). Harpacticoid copepods and cladocerans showed relatively high densities in lake biofilms (135 ± 16.1 ind/10 cm^2), but were largely absent in those of streams, except for S9 (Figure 4b). Also, tardigrades were found at most of the sites (Figure 4c), but were absent in samples from lakes L1, L2, L4 and L9. Early larval stages of chironomids were found at all sites, with densities ranging from 1.2 ± 0.78 ind/10 cm^2 in southernmost lake L1 to 124 ± 19.2 ind/10 cm^2 in northernmost stream S9. Relatively high densities of meiofaunal oligochaetes were only found at sites L4 and L6, that is, 71.7 ± 11.1 ind/10 cm^2 and 72.7 ± 31.2 ind/10 cm^2, respectively (Figure 4d). Cyclopoid copepods were found at low densities in lake biofilms, but were absent in streams (Figure 4d), Ostracods, gastrotrichs and water mites were also found at very low densities in most of the samples (data not shown).

Overall meiofauna biomass was 486.2 ± 90.3 μgDW/10 cm^2 for lakes (range 47.8–1013 μgDW/10 cm^2) and 261.9 ± 94.2 μgDW/10 cm^2 for streams (range 33.3–934 μgDW/10 cm^2) (Table 1), but showed no relationship with latitude (Figure S1). At sites L1, S2, S3 and S5, meiofauna biomass was low. Nematodes, which numerically predominated the meiofauna, also made up a substantial part of meiofauna biomass at most of the sites. Mean nematode biomass for lakes was 123.0 ± 114 μgDW/10 cm^2 (or 25.3% on average) and 46.5 ± 47.0 μgDW/10 cm^2 for streams (or 17.8%).

Nematode biomass in lakes was also equal to or higher (up to 3×) than that of meiofaunal chironomids, that is, their early instars that belong to the temporary meiofauna. Conversely, in all but two of the streams (S4 and S6) mean chironomid biomass exceeded that of nematodes by 2–10 times. Overall mean chironomid biomass was 116.0 ± 22.4 μg/10 cm^2 for lakes and 180.8 ± 83.2 μg/10 cm^2 for streams. Meiofaunal oligochaetes (i.e., true meiofaunal species and juveniles of macrofaunal species) and microcrustaceans (harpacticoids, cladocerans, cyclopoids and ostracods) made up a large share of meiofauna biomass in lakes, but less so in streams (but see S9 and S10). The biomass share of oligochaetes was 15.7% ± 0.1% (range 0%–47%) among lakes and 9.9% ± 0.3% (range 0%–23%) among streams, while corresponding numbers for microcrustaceans were 25.7 ± 0.5 (range 0.4%–70.0%) and 10.6% ± 0.4.0% (range 0.05%–31.6%). Rotifer biomass, despite their high densities, only averaged 2.9% ± 1.8% for lakes and 4.8% ± 1.3% for streams.

Overall meiofauna biomass showed significant linear relationships with both the carbon ($p = 0.0007$, $R^2 = 0.55$) and nitrogen content ($p = 0.0052$, $R^2 = 0.42$) of biofilms (as mgDW/10 cm^2, Figure S2). Similar relationships for the biomass of nematodes, harpacticoid copepods and microcrustaceans (sum of harpacticoids, cladocerans, cyclopoids and ostracods) were also significant ($0.0001 \leq p \leq 0.0174$), but these were entirely dependent on a single outlier (L5) (data not shown). The latter was, however, not true for the overall meiofauna biomass, which still showed highly significant relationships with the carbon and nitrogen content of the biofilm even after site L5 was omitted ($p = 0.033$ for C and 0.052 for N). Meiofauna biomass expressed as carbon units (assuming 50% of dry weight biomass is C) averaged 5.3% ± 1.1% in lakes and 8.1% ± 3.4% in streams, ranging from 2.2% in L5 to 30.1% in S6 (data not shown).

Constrained ordination models showed that ecosystem type explained 33.4%, 68.7% and 47.7% of the explained variation in periphyton, meiofauna and nematode communities, respectively (Table 1), resulting in clear differences between lakes and streams (Figures 5A and 6A,C). Lakes and streams had distinctly different epilithic algal assemblages, with site S10 being an outlier with a strong predominance of filamentous greens and cyanobacteria. Rotifers and tardigrades were more strongly associated with streams and cladocerans and nematodes with lakes. Similarly, for nematodes some genera were strongly associated with lakes (e.g., *Rhabdolaimus*, *Plectus*), whilst others were more common in streams (e.g., *Udonchus*, *Monhystera*). Partialling out the effect of ecosystem type in pCCA and pRDA revealed differences in the main predictors of the three organism groups: Total-P and TOC were important predictors of epilithic algae assemblages, TOC and chloride of meiofauna, and TOC, chloride and elevation of nematode communities (Table 2, Figures 5B and 6B,D). Surprisingly, the climate proxy degreedays did not significantly contribute to any of these models, but TOC was generally correlated with gradients in degreedays (Figures 5B and 6B,D). Nematodes, especially the genera *Udonchus* and *Rhabdolaimus*, were associated with relatively high concentrations of TOC, while *Plectus* and *Punctodora* were more common in ecosystems with relatively high chloride concentrations. Many of the identified cyanobacterial genera represent taxa that are known nitrogen fixers (e.g., *Anabaena, Aphanocapsa, Calothrix, Dichothrix, Stigonema* and *Tolypothrix*).

4 | Discussion

Our study shows that epilithic assemblages of Arctic/alpine lakes and streams are distinctly different, both with regard to primary producers, meiofauna groups and nematode fauna. Although not all meiofaunal groups were determined to lower taxonomic units, the data suggest that epilithic biofilms constitute highly diverse assemblages, which is also confirmed by previous studies (e.g., Dimante-Deimantovica et al. 2016; Walseng et al. 2018). Total-P and TOC were the main predictors of epilithic algal assemblages in pCCA, likely reflecting that their link to nutrients and light climate was stronger than that of climate proxies such as latitude or degreedays. Also, in our pRDA for meiofauna and nematode communities, TOC, chloride and elevation came out as the main predictors. Although elevation partially captured variation in climate, it was surprising that the integrating climate proxy degreedays did not significantly contribute to the variation. However, the observation that degreedays correlated strongly with TOC in constrained ordinations for all groups suggests that TOC, reflecting the share of forests and/or wetlands in the catchment, was a better proxy of local climate along the > 600 km south–north gradient among study sites. However, the concentrations of nutrients and other water chemistry variables were generally low, reflecting ultraoligotrophic, clearwater conditions. The fact that the low chloride concentrations (range 3.6–48 μg/L) were identified as a significant correlate may seem odd but is an effect of sea spray and should be interpreted as a proxy of distance to the Atlantic Ocean. Indeed, the shortest distance of the site to the Atlantic Ocean and mean chloride concentrations showed a highly significant negative relationship ($p = 0.0021$, $R^2 = 0.399$). The fact that higher elevation came out as a significant driver of nematode communities and correlated positively with degreedays and TOC (Figure 6D) is likely due to the fact that some of the sites in the southern end of our latitudinal gradient were at higher elevation (and thus colder).

The estimated mean meiofauna biomass in biofilm samples of 486 ± 90.3 μgDW/10 cm^2 for lakes and 262 ± 94.2 μgDW/10 cm^2 for streams was similar to or exceeded that of epilimnetic zooplankton for these lake types. Zooplankton monitoring data for lakes Abiskojaure, Avundtjärnen, Stor-Björsjön and Gåtejaure for August 2019 showed zooplankton dry weight biomass estimates (assuming DW/WW = 7.5%, Nauwerck 1963) averaged 239 ± 58.6 μgDW/10 cm^2 (range 67.3–352) in the epilimnion

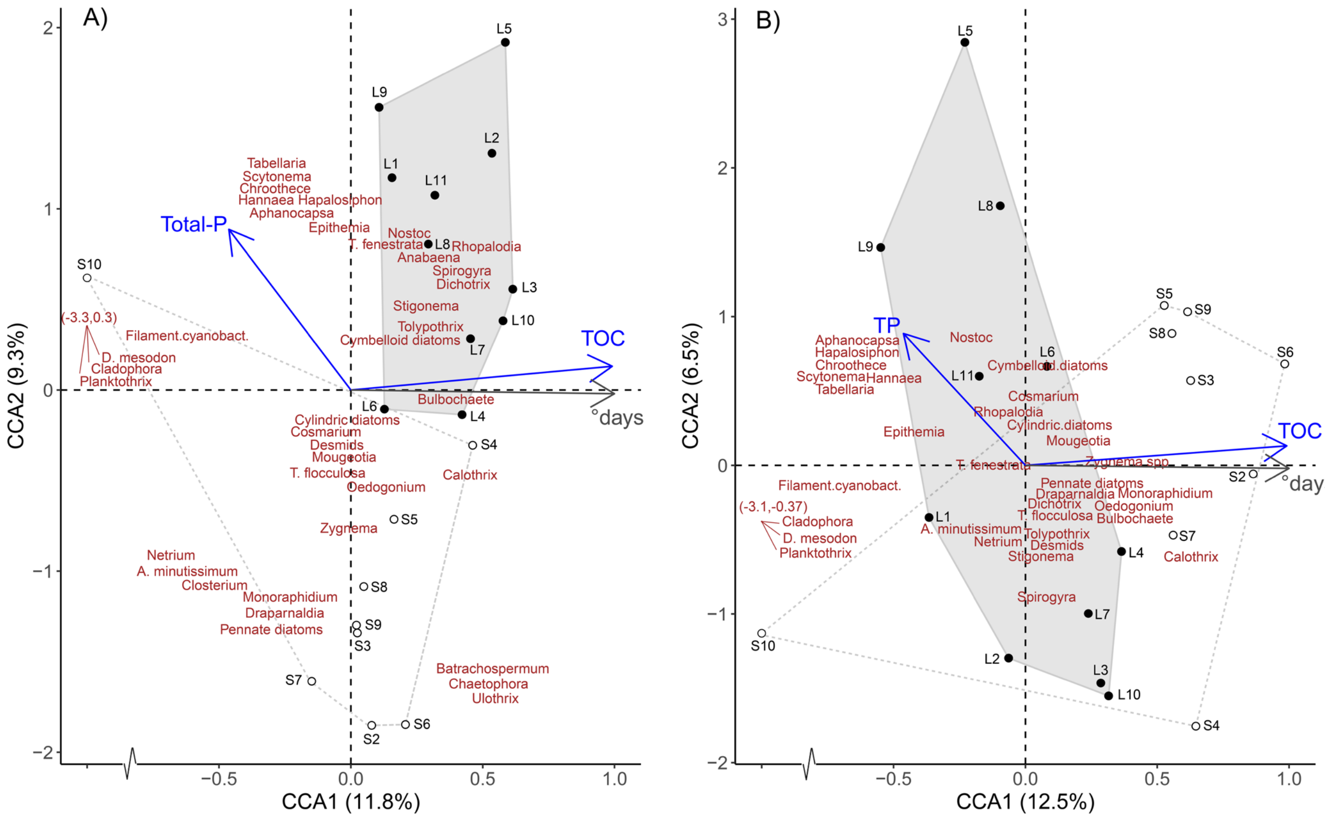

FIGURE 5 | Canonical Correspondance Analysis (A) and partial CCA (B) for the relative biovolume of epilithic algal communities for lakes (black symbols) and streams (white symbols) in relation to significant water chemistry variables (in blue) and degreedays (°days, black arrow). Outlined areas delineate the populations of lakes (grey) and streams (white), respectively. Note the discontinuity of the *X*-axis that was included to visualise site S10 (at −5.4 in left panel and at −5.2 in right panel). Abbreviations have been used for species-level determinations of *Achnanthidium minutissimum* (*A. minutissimum*), *Diatoma mesodon* (*D. mesodon*), *Tabellaria flocculosa* (*T. flocculosa*), Tabellaria fenestrate (*T. fenestrata*). Nostoc refers to *Nostoc* cf. *sphaericum*.

(0–8 m or 8 L over a 10 cm^2 surface) of these lakes (Figure 7). This means the biomass of meiofauna in a few millimetres of epilithic biofilm habitat of lakes exceeds that of zooplankton in an 8-m water column. Similarly, the biovolume of microalgae and cyanobacteria in biofilms of our study lakes is more than 1000-times higher than that of phytoplankton in the epilimnion (0–8 m) of the above-mentioned four monitoring lakes ($1342 \pm 531\ mm^3/10\ cm^2$ in biofilms and $1.12 \pm 0.33\ mm^3$ in an 8 m epilimnion water column). These numbers stress the importance and complexity of the highly compressed biofilm habitat in these clearwater lakes. In addition, while pelagic plankton biomass rapidly declines under the ice, benthic processes proceed during the long, subarctic winter and become a feeding habitat for juvenile stages of pelagic zooplankters such as copepods (Goedkoop and Johnson 1996).

We found no evidence of declining trends in the relative share of cyanobacteria across a south–north gradient for neither lakes nor streams. Primary producers in these ultra-oligotrophic waters were predominated by cyanobacteria in lakes, but less so for streams, where only S4 and S10 had a considerable share of cyanobacteria (> 30%), while the remaining streams had < 2% cyanobacteria. We did, however, find that the highest biovolumes of diatoms, ranging 2214–13,252 $mm^3/10\ cm^2$, were found in the northernmost sites (L7–11, S8 and S9), likely reflecting their adaptation to low-light conditions. Lake biofilms were higher in carbon concentrations than those of streams, but not in algal biovolume. The latter suggests that lake biofilms have more well-developed exopolymeric matrices due to lower hydrological stress and greater stability than those of streams (Resh et al. 1988; Graba et al. 2014). The large share of cyanobacteria, that potentially can fix N_2, in eight of the lakes and two of the streams (Figure 2) confirms that these water bodies may be nitrogen-limited during part of the season, which is in line with earlier findings by Liess et al. (2009) and Diehl et al. (2018).

Nitrogen concentrations in both lakes and streams were extremely low and frequently below the level of detection. All lakes in our study, as well as streams S7, S8 and S10 had a DIN/TP mass ratio < 3.4, that is the transition to P-limitation for phytoplankton growth (Bergström 2010), further suggesting that algal growth was N-limited. All other streams had DIN/TP ratios exceeding 3.4 (range 5.0–32.4) and, consequently, were judged P-limited. Benthic algae, however, will acquire their nutrients both from the overlying water and from nutrient recycling within the biofilms and from underlying sediments (Vadeboncoeur et al. 2006). If instead the criteria for benthic algae in streams by Mebane et al. (2021) are applied (P-limitation if N/P mass ratio > 14, N-limitation if N/P < 10), only stream S10 with an N/P of 6.3 seems N-limited, while S8 with an N/P ratio of 11.4 is judged co-limited. All other water bodies showed N/P ratios exceeding 14 (range 16.7–91.3) and were thus judged P-limited according to

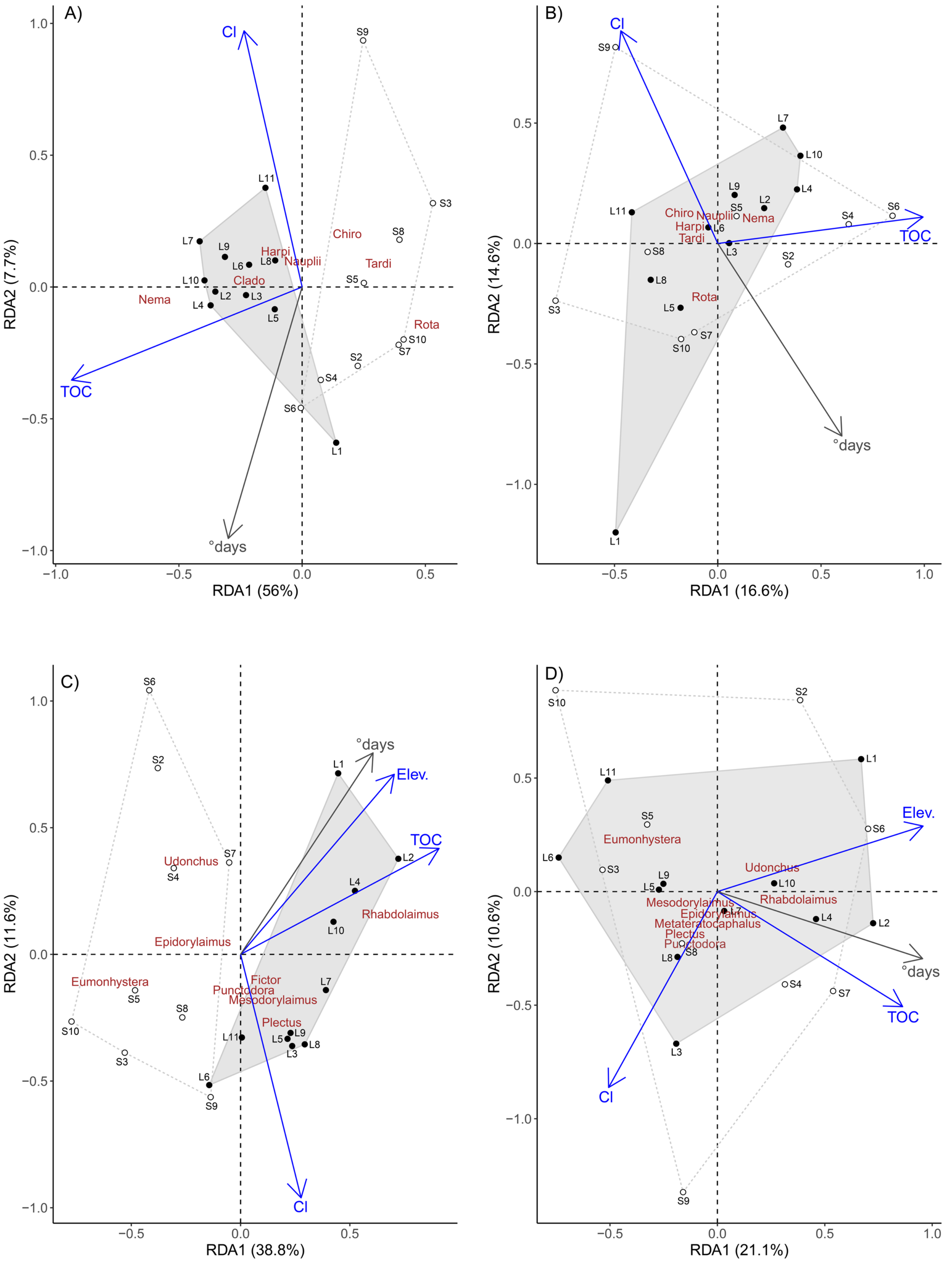

FIGURE 6 | Legend on next page.

FIGURE 6 | Redundancy analysis (RDA) and partial redundancy analysis (pRDA) for the relative abundance of meiofauna groups (A, B) and nematodes (C, D) for lakes (black symbols) and streams (white symbols) in relation significant environmental variables (in blue) and degreedays (°days, black arrow). Outlined areas delineate the populations of lakes (grey) and streams (white), respectively. Logical abbreviations are used for meiofauna groups. Elev. is short for elevation.

TABLE 2 | Constrained multivariate ordination models including full (left) and partial (right) models and the marginal variation (% marg. var.) as well as percentage of explained variation (% var. explained) for significant environmental variables (ANOVA marginal tests, n permutations = 999). Ecosystem type refers to lakes or streams.

Epilithic algae (DCA gradient = 4.19)

CCA→	df	*F*	*p*	% var. marginal	% var. explained	R^2	pCCA →	*p*	% var. explained	R^2
Ecosystem type	1	2.0514	0.002	9.27	33.4	0.269		—	—	0.171
Total-P	1	2.1693	0.034	9.80	35.4			0.047	9.80	
TOC	1	1.915	0.008	8.65	31.2			0.027	8.65	
Residual	16									

Meiofauna (DCA gradient = 0.99)

RDA→	df	*F*	*p*	% var. marginal	% var. explained	R^2	pRDA →	*p*	% var. explained	R^2
Ecosystem type	1	16.0304	0.001	34.46	68.7	0.656		—	—	0.156
TOC	1	3.8419	0.032	8.26	16.5			0.010	8.26	
Cl	1	3.4626	0.042	7.44	14.8			0.014	7.44	
Residual	16									

Nematodes (DCA gradient = 2.00)

RDA→	df	*F*	*p*	% var. marginal	% var. explained	R^2	pRDA →	*p*	% var. explained	R^2
Ecosystem type	1	7.340	0.001	21.41	47.7	0.495		—	—	0.234
TOC	1	3.4013	0.015	9.92	22.1			0.008	9.92	
Cl	1	2.3366	0.065	6.82	15.2			0.045	6.82	
Elevation	1	2.3099	0.067	6.74	15.0			0.048	6.74	
Residual	15									

Mebane et al. (2021). The generally low nitrogen concentrations may, however, still indicate that primary producers of several of these streams and lakes may be nitrogen limited (Myrstener et al. 2017). Cyanobacteria have also developed several biochemical strategies to cope with seasonally low P-concentrations, such as the expression of alkaline phosphatase to access organic P (Adams et al. 2008) and the intra-cellular storage and reuse of polyphosphate (Sanz-Luque et al. 2020). Indeed, Jentzsch et al. (2023) showed that cyanobacteria accumulated poly-P during periods of high phosphate availability, which was then recycled to sustain growth during phosphate scarcity. These physiological adaptations complicate general discussions about nutrient limitations of epilithic assemblages based on nutrient water concentrations and may help explain that we found poor correlations between epilithic assemblage structure and water chemistry variables.

Our hypothesis that densities of meiofauna biomass would decrease across the south–north gradient was also not supported by our data. However, lake meiofauna biomass increased almost linearly between 61.58°N (site L1) and 65.96°N (L6) from 47.8 to 1012.8 μgDW/10 cm^2, then fell back to 166.2 μgDW/10 cm^2 (L7) and again increased linearly to 520.7 μgDW/10 cm^2 at the northernmost site (L11). Stream meiofauna varied between 33.3 (S3) and 398.7 μgDW/10 cm^2 (S7) across the latitudinal gradient, with an exception for site S9 that peaked at 933.9 μgDW/10 cm^2. Meiofauna biomass for both lakes and streams, however, showed significant positive relationships with both the carbon and nitrogen content of biofilms (Figure S2), suggesting accumulated nutrients and habitat structure in the biofilm supported higher meiofauna biomass. Meiofauna biomass was higher for lakes than for streams (*t*-test, $p = 0.0076$), although that of L1, L7 and L8 overlapped with the biomass in the streams (Table 1).

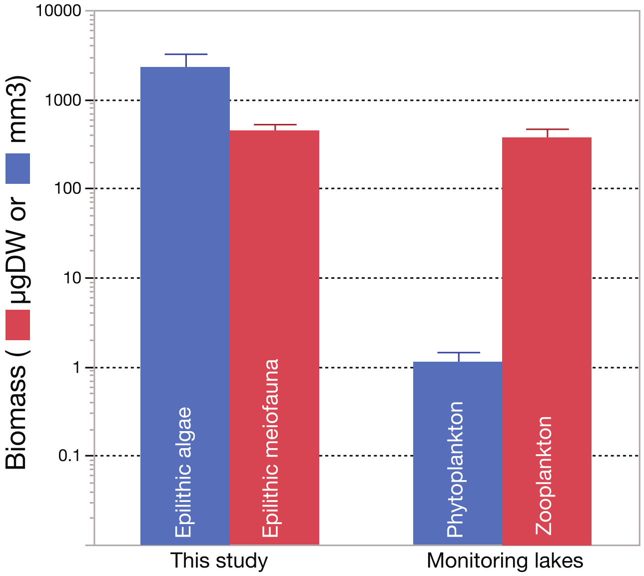

FIGURE 7 | Comparison of the biomass (mean ± 1 standard error) of epilithic algae ($mm^3/10\,cm^2$) with that of integrated epilimnetic (0–8 m) phytoplankton samples in a 10-cm^2 water column ($mm^3/8\,L$ water column) (blue bars) and that of epilithic meiofauna ($\mu gDW/10\,cm^2$) with that of epilimnetic (0–8 m) zooplankton ($\mu gDW/8\,L$ water column) (red bars) for lakes in this study and four oligotrophic Arctic/alpine monitoring lakes in the Scandes (i.e., lakes Abiskojaure, Gåtejaure, Avundstjärnen and Stor Björsjön. NB! That the latter two lakes have also been sampled in the present study). Data from the Swedish National Monitoring Program for August 2019 have been extracted from online data bases (https://miljodata.slu.se/mvm/). For further explanation see the text.

This difference between lakes and streams was mainly due to the higher biomass of microcrustaceans and oligochaetes in lake biofilms. Microcrustaceans, and likely even oligochaetes, can cope less well with the sheer stress of the unidirectional water flow in streams and may find a better habitat in the less disturbed and more well-developed biofilms of lakes. Indeed, our significant relationships between the thickness of biofilms (as mg C/g DW and as mg N/g DW) and meiofauna biomass ($p = 0.0023$) support the role of the biofilm as a habitat and refugia for meiofauna (Majdi et al. 2023). Microcrustaceans such as ostracods and harpacticoids are benthic feeders (Higgins and Thiel 1988), while many cladocerans, such as *Bosmina* and *Chydorus*, can alternate feeding in pelagic and benthic habitats (Rautio and Vincent 2006).

Our study identified 52 and 38 nematode species in biofilm samples from 11 lakes and 9 streams, respectively. Our finding that species richness ranged 7–25 species in the lakes and 3–20 species in the streams agrees well with the 14–22 species identified in the biofilms of three oligotrophic lakes in southern Sweden (Peters and Traunspurger 2005) and the 31 species in oligotrophic lake Largen (Schroeder, Traunspurger, et al. 2012). In biofilms of south Swedish streams 3–32 species were identified (Bighiu et al. 2020), which is also in line with the present study. The nematode community composition in Arctic/alpine lakes and streams not only shows the occurrence of common species (e.g., *Rhabdolaimus terrestris*, *Plectus aquatilis* and *Eumonhystera vulgaris*) but also distinct differences in their densities and habitat preference (Figure 6c, Table S4). Species within these genera were also common in the lake studies by Peters and Traunspurger (2005) and Schroeder, Peters, and Traunspurger (2012). The study of streams in southern Sweden by Bighiu et al. (2020) also had *Eumonhystera* as the most predominant taxon but also found high relative abundances of the bactivorous *Monhystrella* (9%) and the algae-feeder *Chromadorina*, that were absent in our Arctic streams.

Bacteria-feeding nematodes predominated both lake (range 53%–98%) and stream samples (range 56%–100%), supporting the findings by Peters and Traunspurger (2005) and Schroeder, Peters, and Traunspurger (2012). However, in contrast to the Arctic lakes of our study, algae-feeders were considerably more common in the far more nutrient-rich south Swedish lakes, that is, on average 31% (Peters and Traunspurger 2005, Schroeder, Peters, and Traunspurger 2012) and streams, that is, on average 15% (Bighiu et al. 2020). Similarly high proportions of algae feeding taxa were only found in a single Arctic/alpine lake (L3: 29%) and a single stream (S9: 28%). This may seem surprising, as the Arctic lakes and streams are open ecosystems with seemingly autotrophic biofilms. However, the Arctic/alpine ecosystems in our study are also ice covered and dark during 7–8 months per year, thus favouring heterotrophs and disfavoring primary producers. The latter may explain the predominance of bactivorous nematodes in these lakes and streams.

Several studies have shown that the fauna and flora of epilithic biofilms are readily available for grazers and predators and form a strong link to higher trophic levels, especially so in oligotrophic clearwater lakes (see Vadeboncoeur and Power 2017 for review). The algae in biofilms provide grazers with long-chain polyunsaturated fatty acids (PUFA) that are key for efficient growth and reproduction of invertebrates (Müller-Navarra et al. 2000; Goedkoop et al. 2007). In addition, trophic upgrading of detrital carbon through long-chain PUFA synthesis by micro- and meiofauna supplies another trophic pathway (e.g., Menzel et al. 2018; Wallis et al. 2002). Our observed higher $\delta^{15}N$ of stream biofilm samples than those of lakes suggests that stream biofilms provide a higher degree of trophic upgrading among the micro- and meiofauna than those of lakes. This may seem contra-intuitive, as stream biofilms were generally less well developed and had a higher share of potentially nitrogen-fixing cyanobacteria than epilithic lake assemblages (Figure 3), which instead should have contributed to lower $\delta^{15}N$-values. So far we are only just beginning to understand the role of micro- and meiofauna in the trophic upgrading of detrital food at the base of food webs.

4.1 | Outlook

There is currently a strong focus on the climate-induced ecological changes on Arctic ecosystems and its consequences for their unique biodiversity (e.g., Lento et al. 2019; Aronsson et al. 2021). The gradual north migrations of cold-adapted flora and fauna have been described as a 'conveyor belt to extinction' (Goedkoop et al. 2022), an analogue to the 'escalator to extinction' described for bird species along elevation gradients (Freeman et al. 2018). Heino et al. (2020) stressed that many of the ongoing and expected changes of Arctic freshwater ecosystems are irreversible. Unfortunately, freshwater biodiversity estimates tend to focus on human-perceived biodiversity and rarely include the more 'anonymous biodiversity', e.g., the species-rich, smaller fauna of biofilms and sediments (Fenchel and Finlay 2004). Indeed, many micro- and meiofaunal species may go extinct before we even have described them (IPBES 2019). The current, rapid development of barcoding libraries also for smaller fauna should contribute to a better insight into the biodiversity of these relatively unknown groups and their ecological relationships. Our study of high-latitude lakes and streams contributes with baseline knowledge on the littoral, epilithic assemblages and their relationships to key environmental drivers. Our finding that benthic meiofauna biomass exceeds that of water column zooplankton emphasises particularly their relative importance in these ecosystems and in general the importance of benthic processes in clearwater lakes. Our study and data also contribute to a baseline to gauge the effects of climate-induced change on these sensitive ecosystems.

Author Contributions

Conceptualization: W.G. and W.T. Field work: F.C. and W.G. Sample analysis: F.C., S.H., W.T. and K.S.C. Data analysis and interpretation: W.G., S.H., W.T. and F.C. Preparation figures and tables: S.H., W.G. and F.C. Writing: W.G., S.H. and W.T. Commenting/editing: F.C. and K.S.C.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Original data are made available in Supporting Information tables to this manuscript. Monitoring data used for figure 7 are freely available from online data bases at the Swedish University of Agricultural Sciences: https://miljodata.slu.se/mvm/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Sum of meiofauna biomass across latitudinal gradients for lakes (blue) and streams (red). The dashed line shows the position of the Arctic Circle. **Figure S2:** Relationships (linear regressions) between the concentrations of carbon (A) and nitrogen (B) in biofilms and the biomass of meiofauna. Statistical details are given in the panels. Blue and red symbols show lake and stream sites, respectively. The dashed line in the B-panel shows the relationship after removing the outlier (L5), which had a peak in cyanobacteria of $6267.2\,\mathrm{mm}^3/10\,\mathrm{cm}^2$. Statistical details for the dashed line are: $Y = 672.13 * X + 138.9$ ($R^2 = 0.436$, $p = 0.0054$). **Table S1:** Codes, names, coordinates (decimal degrees), as well as morphometric and raw data of annual mean temperature and water chemistry variables of the study sites. L in the site code indicates 'lake' and S 'stream'. 'Size' refers to the area of lakes (in km^2) and the width of streams at the sampling site (in m). Temperature (T) refers to the mean monthly mean daily T for August and July 2021, while degreedays gives the 5-year average (2016–2020) for July–September (±1 SD). Lakes and streams are ordered from south to north. Water chemistry data show the mean of two samples, collected in July and August 2021, except for L1 that was sampled only in September 2020. NB! That for samples of $(NO_2 + NO_3)$-N and NH_4-N concentrations there were below the level of detection (LOD) of 1 and 3 µg/L, respectively, concentrations were set at half the LOD. **Table S2:** Codes, names, as well as raw data of algal biovolumes, C and N concentrations and delta-^{13}C and delta-^{15}N (acidified samples) in biofilms for the study lakes and streams. Note that the locations and other details for the different sites are listed in Table S1. **Table S3:** Site codes, names and meiofauna densities (as $\mathrm{ind}/10\,\mathrm{cm}^2 \pm 1$ standard error) for the study lakes and streams ($n = 5$), as well as their overall mean (±1 SE). Other refer to the sum of Gastrotrichia, Ostracoda and Acari. Note that the locations and other details for the different sites are listed in Table S1. **Table S4:** Site codes (L = lakes, S = streams), nematode richness (and n identified) and densities (as $\mathrm{ind}/10\,\mathrm{cm}^2 \pm 1$ standard error) and relative abundance (as %) of predominant nematode species, that is,

> 10% in either lakes or streams (*Epidorylaimus agilis*, *Eumonhystera vulgaris*, *Plectus aquatilis*, *Rhabdolaimus aquaticus* and *Udonchus* sp.) and functional feeding groups (number and relative share) for the study lakes and streams. Note that the names, locations and other details for the different sites are listed in Table S1. **Table S5:** Nematode species, their densities (as individuals/10 cm^2) and relative abundance (%) in Arctic/alpine lakes (L1—L11) and streams (S2–S10). FT refers to feeding types: AF = algae feeder, BF = bacteria-feeder, OC = omnivorous chewers, OS = omnivorous suction feeder, P = predator, PRF = plant/root/fungi feeder. Note that the names and locations for the different sites are listed in Table S1.