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RESEARCH ARTICLE

Bacterioplankton dispersal and biogeochemical function across Alaskan Arctic catchments

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Abstract

In Arctic catchments, bacterioplankton are dispersed through soils and streams, both of which freeze and thaw/flow in phase, seasonally. To characterize this dispersal and its potential impact on biogeochemistry, we collected bacterioplankton and measured stream physicochemistry during snowmelt and after vegetation senescence across multiple stream orders in alpine, tundra, and tundra-dominated-by-lakes catchments. In all catchments, differences in community composition were associated with seasonal thaw, then attachment status (i.e. free floating or sediment associated), and then stream order. Bacterioplankton taxonomic diversity and richness were elevated in sediment-associated fractions and in higherorder reaches during snowmelt. Families Chthonomonadaceae. Pvrinomonadaceae, and Xiphinematobacteraceae were abundantly different across seasons, while Flavobacteriaceae and Microscillaceae were abundantly different between free-floating and sediment-associated fractions. Physicochemical data suggested there was high iron (Fe⁺) production (alpine catchment); Fe⁺ production and chloride (Cl⁻) removal (tundra catchment); and phosphorus (SRP) removal and ammonium (NH₄⁺) production (lake catchment). In tundra landscapes, these 'hot spots' of Fe⁺ production and Cl⁻ removal accompanied shifts in species richness, while SRP promoted the antecedent community. Our findings suggest that freshet increases bacterial dispersal from headwater catchments to receiving catchments, where bacterioplankton-mineral relations stabilized communities in free-flowing reaches, but bacterioplankton-nutrient relations stabilized those punctuated by lakes.

INTRODUCTION

Water is the primary carrier of microbial organisms through and across landscapes. In upper reaches of a stream network, the stream is comprised largely of water that recently travelled through soil rather than along a stream channel. Soils disperse migrant bacterioplankton that are usually associated with sedimentary particles advected by erosion then entrained (Jamieson et al., 2005), whereas free-floating bacterioplankton are usually natives derived from groundwater or periphyton (Liu et al., 2019). This sediment-associated fraction of bacterioplankton largely controls the composition of the total bacterioplankton community (i.e. sediment-associated plus free-floating fractions), increasing its species diversity (Bishop et al., 2008; Ruiz-Gonzalez et al., 2015; Stadler & del Giorgio, 2022; Widder et al., 2014). As streams converge down the network, there is a relatively smaller contribution of water from soil and an increased residence time of stream water, allowing in-stream physicochemical conditions to remove some terrestrial species and select for aquatic

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species (Liu et al., 2019). Interruptions to stream flow, such as ponds, lakes, and impoundments, increase water residence time and create distinct physicochemical conditions that can increase the longitudinal separation of terrestrial and aquatic species, diluting the soil bacterial signature (Cavaco et al., 2019; Huggett et al., 2017). Thus, stream bacterioplankton communities represent a composite signal of terrestrial and aquatic biogeochemistry in the catchment, though the controls on their spatial variation have not been explored widely in high-latitude regions.

Permafrost regions, which are experiencing some of the most extreme anthropogenic climate change, contain much of the Earth's soil organic matter (Abbott et al., 2022; Cheng et al., 2022; Tank et al., 2020). As these regions thaw, the rate of greenhouse gas production and impact on aquatic and marine environments will be influenced by the microbial community (Ernakovich et al., 2022). Consequently, Arctic regions are both ideal hydrological testbeds for studying microbial dynamics and important bellwethers of ecosystem feedbacks to climate change (Shogren et al., 2020). Arctic catchments offer an opportunity to test how climate change could affect stream microbial communities that interact with a large and currently stable portion of the Earth's organic carbon and nutrients (Abbott, 2022; Keuper et al., 2020; Strauss et al., 2013). In the Arctic, land use is relatively limited (Sanfilippo et al., 2021; Zhao et al., 2021), and there is little to no artificial flow regulation (Jones et al., 2020; Luo et al., 2019), contrasting with most middle and low latitudes (Poff et al., 1997). Permafrost imposes a noflow boundary condition so there is little transport of water from soil to deep groundwater, simplifying the water budget compared to many lower latitude catchments (Rempe & Dietrich, 2018; Shogren et al., 2021).

In the Arctic, permafrost is overlain by a seasonally thawed active layer, which controls how water and bacterioplankton flow through the hydrologic source area and are dispersed through the stream network. The year can be divided into two hydrologic 'seasons'approximately 9 months of frozen surface conditions and 3 months of liquid water flow (Olsson et al., 2003). During a typical frozen season (September–May), rates of biological activity are greatly reduced in the soil, though these rates can still influence annual carbon and nutrient cycles because of the extensive duration of the season (Burkert et al., 2019; Graham et al., 2012; Natali et al., 2019). Precipitation is low and typically falls as snow, so meteoric water is accumulated in the snowpack instead of translated into discharge. When precipitation falls as rain, the water runs off the impermeable hillslope or freezes in place rather than infiltrating into the soil (Forbes et al., 2016). This delivers surface materials, such as aeolian-deposited nutrients, organic matter, and bacteria, directly to the stream network (Stibal et al., 2008). In the transition

into the flow season, the flow rate reaches its maximum, as the melting of accumulated snow and ice creates a 'first flush' (i.e. freshet) that mobilizes surface materials accumulated over the frozen season (Hobbie & Kling, 2014). Throughout the flow season (June-August), surface soils gradually thaw, allowing water to flow deeper in the soil profile and increasing hydrologic connectivity between soil and stream (Harms & Jones, 2012; Neilson et al., 2018). The flow season coincides generally with the growing season, when material (e.g. nutrients and dissolved organic carbon [DOC]) is produced and/or made available to streams (Shogren et al., 2019), impacting bacterioplankton growth and fitness against environmental selection downstream (Malard & Pearce, 2018).

In this study, we investigated the composition, dispersal, and biogeochemical function of bacterioplankton communities throughout natural stream networks in three medium-sized (<100 km²) catchments underlain by continuous permafrost on the North Slope of Alaska. Specifically, we investigated the effects of stream order (a proxy of catchment size and hydrologic residence time), catchment inflection points (e.g. stream confluences, lake inlets, and lake outlets that represent stream/lake mixing), seasonality, landscape type, catchment hydrology, and sediment association of bacterioplankton. We collected bacterioplankton and measured stream physicochemistry at ~60 sites across Alpine, Tundra, and Lake (tundra punctuated by many ponds and lakes) catchments (Figure 1; Table 1; Shogren et al., 2019). To characterize conditions during influential moments in the flow season, we collected samples during snowmelt ('spring') and after vegetation senescence ('fall'; Figures S1-S3). We hypothesized that: (1) bacterioplankton diversity and richness would be highest in the sediment-associated size fraction (>3.0 µm; sestonic and not benthic) in lower stream orders in spring due to high dispersal from soils; (2) bacterioplankton communities would be distinct among catchments and experience a seasonal reversal from dispersal in spring to environmental selection in the fall; and (3) biogeochemical leverage (an estimate of solute production or removal throughout the catchment) would be associated with shifts in bacterioplankton community composition, particularly in lower stream orders in fall where and when bacterioplankton dispersal would be limited.

EXPERIMENTAL PROCEDURES

Study area

We studied three catchments near the Toolik Field Station in the foothills of the North Slope, Brooks Range in Alaska, 254 km north of the Arctic Circle (Figure 1; Table 1). They included a small alpine catchment



FIGURE 1 (A) Map of the three study catchments indicating sampling sites, stream gages, meteorological stations, and Toolik Field Station. (B–D) Close-up maps of (B) Lake (Oksrukuyik Creek), (C) Tundra (Upper Kuparuk River), and (D) Alpine (Trevor Creek) catchments overlaid onto a DEM. Stream order numbers are also presented (stream order 9 is omitted for clarity). (E) Inset map showing the general location of the study area within Alaska.

(Trevor Creek; hereafter 'Alpine'; Figure 1D); a large tundra catchment (Upper Kuparuk River; hereafter 'Tundra'; Figure 1C); and a mid-sized tundra catchment (Oksrukuyik Creek; hereafter 'Lake'; Figure 1B) whose hydrology and biogeochemistry is influenced by lakes (Shogren et al., 2019). The Alpine catchment drains an area of 42.7 km² on the northern slope of the central Brooks Range before flowing into the Atigun River and then into the Sagavanirktok River; the upper part of the catchment is mainly bare bedrock, while peat soils cover the lower reaches (Lehn et al., 2017). The Tundra catchment is 438.7 km², originating in the northern foothills of the Brooks Range, with the streamflow coming almost entirely from overland and subsurface flow in the shallow active layer (McNamara et al., 1998). The Lake catchment is 72.7 km² and drains a cluster of lakes before flowing into the Sagavanirktok River. The Lake catchment is visibly rich with dissolved organic matter (Harvey et al., 1998). In general, the Toolik region is underlain by continuous permafrost (Hamilton, 2003). From 1989 to 2020, mean monthly temperatures ranged from -22.5°C in January (winter) to +11.1°C in July (summer), and mean annual precipitation was 281.9 \pm 18.3 mm, with most falling in the summer between June and September (Toolik Environmental Data Center Team, 2022; Figure S2). Vegetation is moist acidic sedge tundra, moist nonacidic tundra, and shrub tundra (Walker et al., 2005).

Synoptic sampling across stream nétworks

We completed two spatially extensive synoptic sampling campaigns of bacterioplankton and biogeochemistry when the active layer was beginning to thaw on 3 June ('spring') and when the active layer was nearfully thawed on 29 August ('fall') in 2017, each time sampling from the same 58 total sites spread across the three study catchments (Figure 1; Figures S2 and S3; Table 1). At each site, we measured physicochemical parameters (water temperature, pH, conductivity, total dissolved solids, and dissolved oxygen) in-stream using a YSI meter and probe (YSI, Inc., Yellow Springs, Ohio). At each site, we also collected 1 L of stream water in a sterile, triple-rinsed Nalgene bottle. The

TABLE 1 Description of sampling sites

			Confluence	Lake feature		
Site ID	Elevation (m)	Stream order	Yes/no	Inlet/outlet	Drainage area (km	Leverage > 50% (%)
Alpine catchment (Trevo	r Creek: 18 sites)				(
T1 2	1427.3	7			3.2	
T1 3	1431.5	7			0.9	
T3 2	1343.9	8			5.2	
T3 3	1342.2	8			2.6	
T4_3	1232.2	7			2.1	
T4_5	1238.4	5			0.4	
T5 1	1166.8	9	Yes		18.7	Fe ²⁺ (Ps: -69.8)
T6 2	1123.0	5			0.4	
T8_1	1447.9	8			4.4	
T9 2	1423.6	7			1.4	
T9 3	1425.4	7			0.01	
T10 2	1318 7	8			8.0	
T10_3	1329.4	8			3.9	
T11 2	1049.9	9			21.5	Fe ²⁺ (P-: _95 1)
T11 3	1069.9	9			15.5	Fe^{2+} (P ₂ ; -58.1)
T11_3	1065.0	3			0.7	1 e (1 g, -30.1)
T10_1	991.0	4			0.7	
T12_1	061.2	7			42.7	
Tundro octobrant (Unno	902.4				1.2	
rundra calchment (Oppe	ope 4	20 siles)			10.4	
N2_2	986.4	8			10.4	
K2_3	986.8	8			4.8	
K4_2	903.1	9			22.8	
K4_3	903.4	9			4.5	
K5_2	859.9	9	X		24.0	
K5_3	859.5	9	Yes		2.3	
K6_1	885.9	9	Yes	Inlet	17.2	
K8_1	846.7	10	Yes		61.3	
K10_1	862.4	8			4.1	
K11_3	821.7	8			6.8	
K13_1	790.0	10	Yes		101.4	
K13_2	796.5	8			6.3	
K14_3	738.2	9			11.7	- 0.
K14_4	745.5	10			131.4	Fe ²⁺ (P _F ; –61.8)
K16_2	655.6	10			180.9	
K16_3	655.7	8			19.2	Cl [–] (R _F ; 123.3)
K17_4	611.6	7			1.2	
K18_1	543.9	11			438.7	
K18_2	564.5	10			251.8	
K18_3	544.1	8			9.0	
Lake catchment (Oksruk	uyik Creek; 20 site	es)				
01	963.6	7			1.3	
02	895.6	7			2.3	
03	837.6	9			9.2	SRP (R _S ; 76.4)
04	836.4	9			13.9	SRP (R _S ; 192.2)
O5	864.3	7		Inlet	0.8	
O9	849.4	8	Yes		1.5	
013	800.8	7			3.2	

TABLE 1 (Continued)

			Confluence	Lake feature		
Site ID	Elevation (m)	Stream order	Yes/no	Inlet/outlet	Drainage area (km	Leverage > 50% (%)
O14	769.0	10			58.0	$\begin{array}{l} {\sf SRP} \ ({\sf R}_{\sf S}; 498.1), {\sf NH_4}^+ \\ ({\sf P}_{\sf S}; -68.5) \end{array}$
O15	790.3	10			50.5	SRP (R _S ; 359.0), NH ₄ ⁺ (P _S ; -54.8)
O16	811.8	10	Yes		35.7	
O21	869.6	8			2.4	SRP (R _F ; 76.7)
O26	807.8	10			41.7	SRP (R _F ; 57.0), Cl ⁻ (P _F ; -54.5)
O28	818.3	9	Yes		5.7	
O33	838.9	8	Yes	Inlet	6.3	
O35	865.5	7		Outlet	0.6	
O58	757.4	10			72.7	
O59	763.3	10	Yes		69.0	SRP (R _S ; 403.3)
O60	765.3	8			7.1	
O66	839.4	7		Outlet	1.8	
072	843.3	8	Yes		0.6	

Abbreviations: F, fall; P, production; S, spring; R, removal.

water sample was used to further characterize water quality (Turbidity) and chemistry (Ba²⁺, Ca²⁺, Fe⁺, Na⁺, NO₃⁻, NH₄⁺, Si⁴⁺, SRP, TDN, TDP, DOC, and DIC; full results published in the study by Shogren et al., 2019), then the community composition of sestonic bacterioplankton. All samples were transported from the field to a laboratory at the nearby Toolik Field Station, stored at 4°C, then filtered within 6 h. For each sample, 250-1000 ml of water sample was passed through two sequential filters. First, sedimentassociated bacterioplankton were captured with an ashed 3.1 µm glass fibre filter. Second, free-living bacterioplankton were captured with a sterile 0.2 um Supor PES membrane (Pall Corporation, Port Washington, NY). For a minority of sampling sites, there was not enough bacterioplankton material collected for successful DNA sequencing so for every sampling site, there was either zero, one (sediment associated or free floating), or two (sediment associated and free floating) filter samples. After filtration, all filters were stored at -80°C until analysis.

Bacterioplankton DNA extraction and sequencing

We used 16S amplicon DNA sequencing of the filters to identify bacterioplankton communities. We extracted genomic DNA from the filters using the DNEasy Power-Water Kit (Qiagen, Valencia, CA). Then we PCRamplified the V4 region of the bacterioplankton 16 S rRNA gene with primer set 515F and 806R (Caporaso et al., 2010) using dual indices developed by Kozich

et al. (2013). We used thermal cycle conditions of an initial denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 15 s, annealing at 55°C for 30 s, and extension at 68°C for 2 min. After PCR, we normalized the samples using SegualPrep Normalization Plate Kits (Applied Biosystems, Waltham, MA) and pooled them at equimolar concentrations. We submitted the samples for 2 \times 250 bp paired-end sequencing on the Illumina HiSeg 2500 System at the Brigham Young University DNA Sequencing Center (http://dnac.byu.edu/), then processed sequences using the QIIME2 bioinformatics pipeline (version 2018.4; Bolyen et al., 2019). We quality-filtered sequences using DADA2 (Callahan et al., 2016), constructed a phylogenetic tree using fasttree2 (Price et al., 2010), and assigned taxonomy of OTUs at the 97% sequence similarity level against the SILVA database (Quast et al., 2013). We used the decontam package (Davis et al., 2018) in R to identify and remove likely contaminant sequences (e.g. from reagents or handling). We also removed chloroplast and mitochondria sequences. Finally, the dataset was rarefied to 8000 sequences per sample. All sequences are deposited as BioProject PRJNA888129 in NCBI (https://www.ncbi.nlm.nih.gov).

Stream orders and catchment inflection points

We characterized catchment hydrology using GIS data downloaded from the USGS (http://earthexplorer.usgs. gov) and analyses completed in QGIS 3.10. First, raster

Applied Microbiology DEM tiles (1 \times 1 degree; 1/3 arc-sec [~10 m] horizontal resolution: NAD83 horizontal datum: NAVD88 vertical datum) encompassing the study area were downloaded from the National Elevation Dataset. The DEM tiles were merged, warped (i.e. reprojected to a smallerscale Coordinate Reference System, EPSG:6393 [NAD83(2011)/Alaska Albers]), then sink-filled (Wang and Liu algorithm). Then, a channel network was extracted, drainage areas were delineated for all sampling sites, and stream orders were defined. We used the Strahler stream order classification (Strahler, 1952; an nth order stream is always located downstream of the confluence of two [n - 1]th order streams), which is a hierarchy of tributaries that is designed to convey the branching complexity of the catchment, reflecting its morphological structure. Our orders appeared high because the initiation threshold was set to 0 during the creation of the channel network to increase sensitivity to and account for the low-order flowpaths ('water tracks') that predominate in the region (Neilson et al., 2018; O'Conner et al., 2019; Figure S1). Strahler orders are scale dependent and our study catchments were of different sizes, so our sampling sites were on stream reaches with Strahler orders that ranged from 4 to 10 in the Alpine, 7 to 10 in the Lake, and 7 to 11 in the Tundra catchments (Figure S1).

Catchment inflection points (i.e. stream confluences, lake inlets, and lake outlets; Table 1) were identified from satellite images (180×185 km; 30 m horizontal resolution; RGB bands from the Landsat eight data set) that encompassed the study area (Figure 1). Only images of scenes (taken on different days) without cloud cover and terrestrial snow cover were merged and warped, then the abovementioned GIS stream layers were added on to it.

Stream biogeochemistry through leverage

We characterized stream biogeochemistry using a measure of stream chemistry leverage in addition to the raw concentration data. Leverage is a distributed estimate of material flux that may occur at any site along a stream network and then interpreted to infer removal or catchment (Shogren production at the level et al., 2019). While leverage values do not definitively reveal driving mechanisms, they reflect net ecosystem behaviour, creating a metric to identify potential linkages between bacterioplankton community composition and biogeochemical function across spatial scales. The size of source and sink patches were assessed by the spatial scale of the collapse (i.e. reduction) in spatial variance (Abbott et al., 2018). For a given parameter, this spatial variance threshold was expected to occur where subcatchment size matched the size of patches controlling solute production or removal, with downstream reaches less likely to have extreme

concentrations because these sites integrate multiple sink and source patches. The leverage of a subcatchment on outlet chemistry was defined:

$$\text{Leverage}_{S} = (C_{S} - C_{O}) \times A_{S} / A_{O} \times Q_{S} / Q_{O}$$
(1)

where C is the concentration, A is the area, Q is the specific discharge, S is the subcatchment, and O is the outlet. Subcatchment leverage can be expressed in units of percent or proportion because the local subcatchment concentration is normalized to outlet concentration, and it may be interpreted as the contribution of the subcatchment to catchment-level mass flux. At the site level, a positive leverage value indicates a source, and a negative leverage value indicates a sink relative to the outlet (Abbott et al., 2018). At the catchment level, a mean positive leverage indicates net uptake or removal (there are more sources in the subcatchments than can be accounted for at the outlet), whereas a mean negative leverage indicates net release or production. A mean leverage near zero indicates conservative mixing with no net removal or production.

Bacterioplankton community characterization

Bacterioplankton communities were evaluated with Alpha diversity metrics, multivariate statistics, and taxonomical differences. All statistics were done in the R software environment. First, we calculated richness or the number of OTUs in a community because it is the most intuitive and natural index of diversity. However, richness weights all species equally independent from their relative abundances so that rare species count equally to common species and are more likely to be undetected. We also calculated the Shannon Diversity index (Shannon, 1948) because it considers both species richness and evenness. We analysed richness and diversity by subsetting the bacterioplankton community data set according to sediment association, season, and catchment. To compare these subsets of univariate data easily, they (and leverage data) were displayed as bean plots (Figures 3 and 4; Kampstra, 2008). In each bean, the individual observations of data, their mean value, and a kernel density estimate of their distribution are shown. In this visualization, anomalies in the data, such as bimodal distributions, are easily spotted. Specifically, we used asymmetric bean plots to compare two primary subgroups (spring and fall). Additionally, we used ANOVA to identify differences between diversity and richness according to sediment-association, catchment, season, and stream order.

Second, we used the *phyloseq* package (McMurdie & Holmes, 2013) to create principal coordinate analysis (PcoA) plots and permutational

multivariate analysis of variance (PERMANOVA) matrices. The PcoA and PERMANOVA visualized and identified differences in bacterioplankton communities across catchments, seasons, and specific locations within the stream network. We used the vegan package (Dixon, 2003) to generate Bray-Curtis distance matrices, then used the 'adonis' algorithm to calculate the sums of squares to generate dissimilarity matrices. Additionally, we performed redundancy analyses (RDA) to relate bacterioplankton communities to measured biogeochemical leveraging. RDAs were completed for each catchment. Predictor types included all leverage variables: CI^- , Na^+ , Ca^{2+} , Ba^{2+} , Ca^{2+}/Na^+ , Ca²⁺/Ba²⁺, DOC, NO₃⁻, NH₄⁺, TDN, SRP, TDP, Fe²⁺, and Si⁺. All leverage scores were first checked for collinearity (using the variance inflation factor in the usdm package) and normal distributions (using the Shapiro-Wilk test). The RDAs used weighted UniFrac distance matrices to account for relative abundance of each of the OTUs. Forward stepwise RDA models were built with significance (α) set to 0.1 rather than 0.05 to allow for more interactions between variables to be identified.

Third, we evaluated differences in bacterioplankton taxonomical abundance in each catchment by stream order and location. Venn diagrams were generated to evaluate the shared and unique OTUs in bacterioplankton communities separated by catchment, season, and sediment association. These diagrams were generated for all sampling sites and then separately for locations with high leverage (i.e. hot spots).

RESULTS

Bacterioplankton community composition

Across all study catchments, the compositions of bacterioplankton communities were dominated by 16 families with a relative recovery above 0.05% (Figure S4). Overall, the most abundant families were *Burkholderiaceae* (Betaproteobacteria), *Chthoniobacteraceae* (Verrucomicrobia), *Flavobacteriaceae* (Bacteroidetes), and *Omnitrophaceae* (Verrucomicrobia). Of these, the most abundant family was *Burkholderiaceae*, which dominated the community composition of the Tundra and Lake catchments, but not the Alpine catchment.

We used analysis of compositions of microbiomes with bias correction (ANCOM-BC; adj. *p* < 0.05) to identify families whose relative abundances were significantly different across catchments, seasons, and sediment-association status. The families *Chthonomonadaceae* (Armatimonadetes), *Pyrinomonadaceae* (Elusimicrobia), *WD260* (Gammaproteobacteria), and *Xiphinematobacteraceae* (Verrumicrobia) exhibited relative abundance differences in spring relative to fall in all catchments (Figures S5–S7). The families *A4b* (Chloroflexi), *Flavobacteriaceae* (Bacteroidetes), and *Microscillaceae* (Bacteroidetes) exhibited relative abundance differences in sediment-associated relative to free-floating fractions in all catchments (Figures S8–S10).

Influence of seasonal hydrology, landscape type, and sediment association

Many Arctic waterways have low-order preferential flowpaths called water tracks (Neilson et al., 2018; O'Conner et al., 2019), so we used a modified Strahler method to calculate stream order, which accounted for water tracks (Figure S1). Species composition of bacterioplankton communities was distinct among all study catchments, and the combination of season, sediment association, and stream order intensified differences (Figure 2). Based on a three-way interaction in PCoA and PERMANOVA, season, catchment, and sediment association (F = 1.4, $R^2 = 0.01$, p < 0.02) structured communities. Season (F = 24, $R^2 = 0.09$, p < 0.001; Figure 2A) had the strongest influence on communities, followed by catchment ($F = 10, R^2 = 0.08, p < 0.001$) and sediment association (F = 8.1, $R^2 = 0.03$, p < 0.001; Figure 2B). When stream order was considered, communities were structured by stream order and catchment, especially in the Alpine catchment (stream order × catchment: F = 1.4, $R^2 = 0.03$, p < 0.001; Figure 2C), and by stream order and season (stream order \times season: F = 1.3, $R^2 = 0.03$, p = 0.003), although these factors still explained a small proportion of the total variation between samples.

Species diversity and richness

Across all study catchments, the Shannon diversity of bacterioplankton was elevated in the sedimentassociated fraction, in higher stream orders, and in spring. When sediment-associated and free-floating fractions were combined, catchments had a similar level of diversity (four-way ANOVA, catchment, F = 1.18, p = 0.31, df = 2). For only the sedimentassociated fraction, means (±standard errors) were 6.46 ± 0.06 in Alpine, 6.13 ± 0.15 in Tundra, and 6.04 ± 0.13 in Lake catchments in spring; means were 5.94 ± 0.16 in Alpine, 6.06 ± 0.16 in Tundra, and 6.12 ± 0.14 in Lake catchments in fall. Diversity was 5%-13% higher in the sediment-associated than freefloating fraction, and diversity in the free-floating fraction was 11% higher in spring than fall (four-way ANOVA, sediment association \times season, F = 5.8, p = 0.017, df = 1; Figure 3A). Diversity was also influenced by stream order in conjunction with season, as 7th, 9th, and 11th order streams supported at least 13% higher diversity in spring (four-way ANOVA, stream order \times season, F = 2.4, p = 0.028, df = 6;





FIGURE 2 PCoA for all study catchments. Variables included (A) season \times catchment, (B) season \times sediment association, and (C) stream order \times catchment. PERMANOVA results showed that bacterioplankton communities were clustered first by season followed by catchment, sediment association, and stream order.

Figure 3C). In spring, diversity increased with stream order, but in fall, the opposite trend was apparent (Figure 3C).

Sediment association and higher stream orders in spring supported elevated levels of taxonomic richness. Similar to diversity, when sediment-associated and free-floating fractions were combined, catchments had a similar level of richness (four-way ANOVA, catchment, F = 0.88, p = 0.42, df = 2). For the sediment-associated fraction, means were 1039.3 \pm 54.7 in Alpine, 915.5 \pm 116.4 in Tundra, and 888.9 \pm 88.4 in Lake catchments in spring; means were 886.2 \pm 127.5 in Alpine, 942.4 \pm 102.7 in Tundra, and 989.9 \pm 115.7 in Lake catchments in fall. Richness was 1.3 times

higher in the sediment-associated compared to the free-floating fraction (four-way ANOVA, sediment association, F = 16, p < 0.001, df = 1; Figure 3B). Also, richness was at least 20% higher in spring in 7th, 9th, and 11th order streams (four-way ANOVA, stream order × season, F = 3.3, p = 0.005, df = 6; Figure 3D). In spring, richness (like diversity) increased with stream order, but in fall, the opposite trend was apparent (Figure 3D).

Linkages between bacterioplankton community composition and biogeochemical function

We estimated production and removal of solutes with an ecohydrological metric called leverage (Frei et al., 2021). We observed a wide range of positive (removal/uptake) and negative (production/release) leverage values throughout all study catchments in both spring and fall (Figure 4). However, biogeochemical hot spots, which we defined as exhibiting at least a 50% change (increase or decrease) in mass relative to the catchment outlet, occurred only in streams with an order of 8 or higher (Table 1). Hot spots occurred at 15 of the 116 total sampling sites (i.e. 58 sites sampled in spring plus the same 58 sites sampled again in fall); only 2 (of 15) occurred in stream confluences and none occurred in lake inlets or outlets. The Lake catchment supported the largest number of hot spots (10/40 sampling sites in the catchment). Here in the Lake catchment, 7 (of 10) were associated with removal of soluble reactive phosphorus (SRP), more in spring (5 hot spots) than fall (2 hot spots). There were two hot spots for production of NH4+ in spring (co-located with removal of SRP), and one for production of Cl⁻ in fall. Also in the Lake catchment, seven hot spots occurred in 10th order streams. The Alpine catchment had only three hot spots of 36 sampling sites in the catchment, all associated with production of Fe⁺ in ninth order streams in spring or the removal of Cl⁻ in an eighth order stream in fall. This suggests more conservative transport of solutes and less microbial activity.

Bacterioplankton richness, particularly in the sediment-associated fraction, was associated with hot spots (e.g. Fe⁺ in the Alpine catchment; Fe⁺ and Cl⁻ in the Tundra catchment; and SRP and NH₄⁺ in the Lake catchment; Figures 5 and 6; Table 1). This pattern was pronounced in the Lake catchment in spring, for which linear regression models showed that SRP leverage was positively associated with richness in the sediment-associated fraction ($R^2 = 0.32$, p < 0.05; Figure 5) and negatively associated (though the relationship was not statistically significant) in the free-floating fraction ($R^2 = 0.13$, p = 0.12; Figure 5). There was no similar relationship between SRP leverage and diversity, nor between other hot spot variables



FIGURE 3 Distributions of bacterioplankton species (Shannon) diversity and richness across the three study catchments (i.e. Alpine, Tundra, and Lake). Results are separated by (A) season and sediment association; (B) sediment association only; and (C, D) stream order and season. Inside each bean plot, lines identify the frequency of observation points, the bean area shows the distribution of points as a nonparametric Gaussian kernel density shape, and the bold line shows the mean of the distribution.

(i.e. Fe^+ , CI^- , and NH_4^+) and richness nor diversity. Here in the Lake catchment, Venn diagrams of richness at the most active hot spots showed that high SRP leverage promoted the same community in which 59% of the taxa were shared between the hot spot and next downstream sampling site (Figure 7). Conversely, in the Alpine and Tundra catchments, Fe⁺ (Alpine) and Cl⁻ (Tundra) hot spots resulted in an increase in richness with only 30% (Alpine) and 20% (Tundra) of taxa shared between the hot spot and next downstream sampling site (Figure 7).

We made redundancy analysis (RDA) models for each catchment and season to relate biogeochemical activity to bacterioplankton community composition. Relationships were significant only in the Alpine and Lake catchments, only in spring, and only for the freefloating fraction. Importantly, none of these relationships, which were calculated at the catchment scale, were associated with hot spot variables identified at the point/reach scale (Table 2). Specifically, in the Alpine

catchment in spring, Fe⁺ hot spots were common, but the RDA model ($R^2 = 0.18$) suggested that high concentrations of NO3⁻ and DOC structured free-floating bacterioplankton communities. In the Lake catchment in spring, SRP hot spots were common, but the RDA model ($R^2 = 0.21$) showed that high concentrations of Fe⁺ structured free-floating communities.

DISCUSSION

Communities of bacterioplankton are structured largely by two mechanisms-dispersal with hydrologic flow (Albright & Martiny, 2018; Crump et al., 2007; Crump et al., 2012; Findlay, 2010) and subsequent environmental selection by physicochemical conditions in the stream (Fierer & Lennon, 2011; Jones et al., 2020; Zwart et al., 2002). Both are influenced by the residence time of water, which determines the timing of dispersal and moderates environmental



FIGURE 4 Distributions of leverage for Fe²⁺, Cl⁻, and SRP (i.e. the nutrients with the largest values of leverage for the Alpine, Tundra, and Lake catchments, respectively). The grey dashed line indicates a leverage of 0%. Positive values of leverage indicate mineral/nutrient removal, whereas negative values indicate mineral/ nutrient production.

selection (Ben Maamar et al., 2015; Jones et al., 2020; Niño-García et al., 2016). In lowproductivity ecosystems with long residence times, environmental selection is important but may operate only on taxa that were successfully dispersed from soils and then persisted downstream. For example, in Boreal Canada, the proportion of soil-derived bacterioplankton species was seldom lower than 70% even in the systems with relatively long water residence times (>1000 days; Ruiz-Gonzalez et al., 2015). In Arctic tundra and Boreal forest, the composition of riverine bacterioplankton communities often depends on changes in the flow rate that mobilize soil sources of otherwise sessile bacterioplankton as potential instream inoculum, rather than on environmental selection (Cavaco et al., 2019; Crump et al., 2012). Given the importance of hydrologic discharge on the rate of inoculation from terrestrial environments and the distribution of residence time in the stream network (Abbott et al., 2016; Burt & Pinay, 2005), we investigated the role of permafrost hydrology on bacterioplankton dispersal, composition, and function, and,

indirectly, in-soil processing and hydrologic transport of edaphic material.

Spatially homogenous dispersal of bacterioplankton within catchments across the flow season

We hypothesized that bacterioplankton diversity and richness would be highest in the sediment-associated fraction in lower stream orders in spring due to high dispersal from soils. Our hypothesis was supported partially as bacterioplankton diversity and richness were higher in sediment-associated fractions, but these differences occurred only in higher stream orders in spring or else across stream orders in fall (Figures 2 and 3). The sediment association suggests dispersal mechanisms were important, but there may have been specific conditions on dispersal, such as spatial homogeneity in the contribution of flow from the landscape in both spring and fall. In spring, there was extensive snow cover and very shallow thaw depth, so the soilstream connection was strong throughout the whole catchment, not only in smaller streams. Then, through most of the flow season, it was likely that water tracks routed water and materials near the soil surface directly to the stream network (Harms et al., 2021; Trochim et al., 2016). These water tracks are known to predominate across the landscape (Harms & Ludwig, 2016). As thaw depth increased (Figure S3), it was likely that more subsurface material was made available (Natali et al., 2019; Treat et al., 2016). By fall, the ground was near maximally thawed and likely had the highest subsurface hydraulic conductivity of the year, so taxa were still beina contributed from across the whole catchment.

In support of this interpretation of spatial homogeneity in dispersal was the weak effect of stream order on bacterioplankton composition, diversity, and richness (ANOVA results and Figures S11 and S12). This weak effect also suggested diversity and richness were enhanced everywhere by broad environmental conditions, such as seasonal warming in spring, then other stream water conditions in fall. However, in our analyses, the effect of stream order was measured only within each catchment, not across catchments, and catchments themselves were a statistically important variable in structuring bacterioplankton composition. Furthermore, in spring, diversity and richness were highest (for both sediment-associated and free-floating fractions) in the Alpine catchment relative to the Tundra and Lake catchments (Figure 3). Therefore, diversity and richness of bacterioplankton communities likely decreased with increasing travel distance from their common origin in headwater surface soils (Liu et al., 2019), but doing so at the basin scale across catchments with different landscape positions, vegetation cover, and hydrology.



FIGURE 5 Scatter plots of leverage of SRP versus bacterioplankton species richness. The relationship was statistically significant in spring for the sediment-associated fraction ($R^2 = 0.32$, p < 0.05; orange solid line) but not for the free-floating fraction ($R^2 = 0.13$, p = 0.12; orange dashed line). The grey dashed line indicates a leverage of 0%. Positive values of leverage indicate SRP removal, whereas negative values indicate SRP production.

Catchment hydrology causes seasonal shift from dispersal to selection control

We hypothesized that bacterioplankton communities would be distinct among catchments and experience a seasonal reversal from dispersal to environmental selection dominating through the flow season. Our hypothesis was supported with a few caveats. First, bacterioplankton communities were distinct in the spring and fall (Figures S5-S7) and between sedimentassociated and free-floating fractions (Figures S8–S10) within their respective catchments. Second, the Tundra and Lake catchments were similar to each other, whereas the Alpine catchment was distinct. Surprisingly, in fall, diversity and richness were higher in the Tundra (for the free-floating fraction) and Lake catchments (for the sediment-associated fraction), rather than in the Alpine catchment (as in the spring; indicated by mean values given for each catchment above). Also, in the sediment-associated fraction, there was an increase in richness in Tundra and Lake catchments and an increase in diversity in the Lake catchment from

spring to fall, but there was no increase in either richness nor diversity in the Alpine catchment. In the freefloating fraction, there was a decrease in diversity and richness in all catchments. All this indicates that only in the Alpine catchment, there may have been high selection pressures reducing diversity, despite the ongoing dispersal of more diverse bacteria through subsurface flow paths from the thawing soil.

Bacterioplankton dispersal linked to stream biogeochemistry at hot spots

We hypothesized that biogeochemical activity (i.e. solute production/removal measured as leverage) would be associated with shifts in bacterioplankton communities, particularly in lower stream orders in fall when bacterioplankton dispersal is limited. Contrary to our hypothesis, the RDAs (Table 2) did not identify biogeochemical leverage as an important predictor of bacterioplankton community structure at the catchment scale. Often, the biogeochemistry in headwater



FIGURE 6 Maps of leverage (Fe^{2+} , Cl^- , and SRP) and bacterioplankton species richness showing the locations of hot spots and the timing of hot moments. Positive values (blue) of leverage indicate mineral/nutrient removal, whereas negative values (red) indicate mineral/nutrient production.

streams resembles the soil solution from which they derive, but larger rivers show quite different conditions (Abbott et al., 2018; Creed et al., 2015; Zarnetske et al., 2018); thus, investigating biogeochemical mechanisms requires a spatially explicit, network approach (Shogren et al., 2019). When we analysed catchments at the point/reach scale by season, it appeared that leverage hot spots were important (Figures 4–7; Table 1).

In the Alpine catchment, consistent biogeochemical activity occurred across the flow season, as Fe⁺ was produced at two hot spots in spring and at another one in fall. Previous ecohydrological work in this catchment has shown seasonal trends from increasing thaw depth and physical weathering of the geologically young sediment (Lehn et al., 2017). This suggests the importance of superficial landscape characteristics (e.g. vegetation, soil, and surficial geology) as state factors in the composition of bacterioplankton communities. Landscape characteristics control the storage and routing of water, which drive the production and availability of nutrients and DOC, which in turn are crucial for bacterioplankton growth and function against environmental selection downstream (Malard & Pearce, 2018). Simultaneously, environmental selection affects the composition (i.e. absolute makeup and relative diversity of taxonomy) of a bacterioplankton community and its functional ability to affect the local

biogeochemistry, such as the decomposition of biological material, delivery of nutrients and DOC to surface waters, and generation of greenhouse gases (Harms et al., 2020; Malard & Pearce, 2018; Monteaux et al., 2020).

The Tundra and abutting Lake catchments, which had similar landscape position, soil, vegetation cover, and stream networks, showed very different (relative to the Alpine catchment) biogeochemical activity. In the Tundra catchment, there was biogeochemical activity potentially associated with surficial geology only in fall, when Fe⁺ was produced at one hot spot (stream order = 10) and Cl^- was removed at another (stream order = 8). In the Lake catchment, there were hot spots in higher stream orders (9 and 10), but they were primarily nutrient-driven alterations, unlike the other catchments. In spring, when subsurface hydrologic systems were not connected to the stream network, SRP was being removed at seven hot spots. Two of these hot spots (stream order = 10) were co-located with NH_4^+ production. The most active hot spot of all sampling sites and in both spring and fall occurred, removing SRP and producing NH₄⁺ in a 10th ordered stream downstream of lakes and ponds and near the catchment outlet (Figure 6). Concomitantly, the leverage in the Lake catchment resulted in an increase in bacterioplankton richness downstream of this hot spot (Figure 7). All this indicated there was low longitudinal



FIGURE 7 Venn diagrams of bacterioplankton species richness for the sediment-associated fraction at (A) the hottest hot spots of biogeochemical activity in Alpine (TC11.2; Fe^{2+} leverage = -95.1), Tundra (KUP16.3; CI^- leverage = 123.3), and Lake (OKS14; SRP leverage = 498.1) catchments with their immediately upstream and/or downstream sites (each hot spot was hot only in spring or fall, but not both, so the hot spot location is also referred to generally as a 'site of interest'), and (B) all sampling sites combined within catchments. Positive values of leverage indicate mineral/nutrient removal, whereas negative values indicate mineral/nutrient production.

TABLE 2 RDA model results

Catchment	Season	Predictor type	Predictor variables	R ²
Alpine	Spring	Leverage	$NO_3^{-\star} + DOC +$	0.18
Lake	Spring	Leverage	Fe ²⁺ *	0.21

Note: Predictor types included: CI^- , Na^+ , Ca^{2+} , Ba^{2+} , Ca^{2+}/Na^+ , Ca^{2+}/Ba^{2+} , DOC, NO_3^- , NH_4^+ , TDN, SRP, TDP, Fe^{2+} , and Si^+ . *p < 0.05;

continuity of nutrient flux (conversely, high rates of material retention and release), but high rates of bacterioplankton flux (i.e. dispersal). The stream microbial community is likely phosphorus (P)-limited, based on studies in nearby stream (Harms et al., 2019; Harms & Ludwig, 2016) and lake (Slavik et al., 2004) ecosystems on the North Slope. This indicates that P concentration could be controlled primarily by immobilization in the aquatic environment (Shogren et al., 2019). The overall retention of SRP throughout the catchments could be the combined effect of physical retention and bacterioplankton assimilation, as P is often considered a universal limiting nutrient. In fall, when subsurface soil flow paths were connected to the stream network, only two of the same SRP hot spots (which were not producing NH_{4}^{+}) were still removing SRP. Surprisingly, none of these hot spots were at stream confluences or lake outlets, which have been observed to influence biogeochemical transformations in other environments (Larned et al., 2011; McClain et al., 2003).

It is important to note that in our study, some connections between bacterioplankton and stream biogeochemistry may be obscured by high rates of metabolic dormancy in these communities (Hall et al., 2018). Because our study profiled total bacterioplankton communities using DNA amplicon sequencing, we could not distinguish between metabolically active and dormant taxa, the latter of which would not influence the production or removal of stream solutes. Only a subset of the total community is metabolically active in streams, with the majority of taxa being passively dispersed or unreactive (Stadler & del Giorgio, 2022; Wisnoski et al., 2020). This could explain the apparent lack of relationship between bacterioplankton community composition and biogeochemical hot spots for some parameters. More active taxa could have emerged at specific points and times (e.g. in the Lake catchment in spring), but RNA sequencing or other activity-focused measures would be required to confirm the metabolisms driving these patterns.

Implications of bacterioplankton dispersal on carbon feedbacks in a changing Arctic

The composition, dispersal, and biogeochemical function of bacterioplankton can reduce or amplify the lateral transport of carbon and nutrients (Bernhardt et al., 2017; Besemer et al., 2013; Frei et al., 2021). To further our understanding of carbon dynamics, catchment and basin hydrology remain a high priority in Arctic research. Changes to the water balance are a major source of uncertainty in the hydrologic dispersal of bacterioplankton and export of DOC (Abbott et al., 2016; Osuch et al., 2022; Vonk et al., 2019). High nival flows and source areas have been shown to be important in

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seeding and inoculating downstream communities (Battin et al., 2001). A change in climate could affect the timing and magnitude of stream flow, which could shift the bacterioplankton community to a late-season community earlier, potentially affecting transport and processing of carbon and nutrients. Downstream in the stream network, hydrologic interruptions to stream flow are in flux. Pond area and abundance have been reported to be decreasing in Arctic tundra (Andresen & Lougheed, 2015). Moreover, permafrost thaw is triggering rapid changes in the landscape (e.g. through thermokarst formation), resulting in drainage and flooding of different areas in the stream network, fundamentally changing water residence time and physicochemical characteristics of the water column (Abbott et al., 2022; Wologo et al., 2021).

In this and previous work in these catchments (Shogren et al., 2019, 2020, 2021), we did not observe any hot spots of DOC leverage, nor did we see any relationships between DOC leverage and bacterioplankton community structure in the RDAs. However, the most abundant families in the study catchments were chemoheterotrophs known to utilize organic carbon in sediments or suspended in the water column. For example, the Burkholderiaceae (Betaproteobacteria) are common in Arctic tundra and assimilate cellobiose even under subzero temperatures (Gadkari et al., 2020). The Pyrinomonadaceae and Xiphinematobacteraceae were more abundant in spring, suggesting that these taxa capitalized on the first flush of organic carbon. The Chthoniobacteraceae (Verrucom icrobia) are commonly associated with plant-rich soils and are abundant in sediment-associated communities, especially during the growing season (Wang et al., 2019). The Flavobacteriaceae are potentially psychrotolerant, utilizing carbon common in soils and river sediments (Begum et al., 2013; Chaudhary et al., 2019). Alternatively, the A4b, Flavobacteriaceae, and Microscillaceae are commonly associated with suspended sediments. While these processes are doubtless at play in these catchments, the combination of low residence time and relatively high DOC concentrations likely limited their effect on DOC mass balance (Abbott et al., 2016).

The fate of DOC pools is dependent on both biogeochemical processing by bacterioplankton, and on the diversity and quality of dissolved organic matter (DOM) substrate. This diversity and quality can be higher in the headwaters relative to downstream locations in continuous permafrost regions (Vonk et al., 2015), though this pattern can vary depending on periglacial history, DOM source, and vegetation type (Tank et al., 2020; Wologo et al., 2021). Also, permafrost contains such large pools of organic carbon and nutrients that the release of terrestrial material and its interaction with microorganisms in the soil and surface water networks can lead to different DOM composition and distinct microbial communities in distant coastal waters at the end of the stream network (Bruhn et al., 2021). Release of DOC from permafrost may also increase the mineralization rates of more recalcitrant stream organic matter via priming effects, with potential consequences for local aquatic habitat, marine productivity in the Arctic Ocean, and global biogeochemical cycles (Abbott et al., 2022; Wologo et al., 2021). The use of fluorescence spectroscopy coupled with parallel factor (PARAFAC) analysis is a promising avenue to investigate sources of DOM (Mann et al., 2016). Combining DOM characteristics with bacterioplankton community (Danczak et al., 2021) could shed light on important two-way interactions between the quality of DOM and the dynamics of bacterioplankton dispersal.

AUTHOR CONTRIBUTIONS

Raymond Lee: Conceptualization (equal), Formal Analysis (equal), Investigation (equal), Methodology Project Administration (lead), (equal). Validation (equal), Visualization (lead), Writing-Original Draft Preparation (lead), Writing-Review & Editing (lead). Natasha Griffin: Conceptualization (equal), Data Curation (equal), Formal Analysis (equal), Investigation (equal), Methodology (equal), Validation (equal), Visualization (equal), Writing-Original Draft Preparation (supporting), Writing-Review & Editing (equal). Erin Jones: Conceptualization (equal), Data Curation (equal), Formal Analysis (equal), Investigation (equal), Methodology (equal), Visualization (equal). Benjamin Abbott: Conceptualization (equal), Data Curation Supervision (equal), Funding Acquisition (equal), (equal), Writing-Review & Editing (equal). Rebecca Frei: Writing-Review & Editing (supporting). Samuel Bratsman: Visualization (supporting). Mary Proteau: Data Curation (supporting). Isabella Errigo: Data Curation (supporting). Arial Shogren: Data Curation (supporting). William Bowden: Data Curation (supporting), Funding Acquisition (equal). Jay Zarnetske: Data Curation (supporting), Funding Acquisition (equal). Zachary Aanderud: Conceptualization (equal), Data Curation (equal), Formal Analysis (equal), Funding Acquisition (equal), Investigation (equal), Methodology (equal), Resources (lead), Supervision (equal), Validation (equal), Writing-Review & Editing (equal).

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the National Center for Biotechnology Information at https://www.ncbi.nlm.nih.gov, reference number BioProject PRJNA888129.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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