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ARTICLE

Freshwater Ecology

Linking permafrost to the abundance, biomass, and energy density of fish in Arctic headwater streams

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Abstract

Permafrost thaw alters groundwater flow, river hydrology, stream-catchment interactions, and the availability of carbon and nutrients in headwater streams. The impact of permafrost on watershed hydrology and biogeochemistry of headwater streams has been demonstrated, but there is little understanding of how permafrost influences fish in these ecosystems. We examined relations among permafrost characteristics, the resulting changes in water temperature, stream hydrology (e.g., discharge flashiness), and macroinvertebrates, with the abundance, biomass, and energy density of juvenile Dolly Varden (*Salvelinus malma*) and Arctic Grayling (*Thymallus arcticus*) across 10 headwater streams in northwestern Alaska. Macroinvertebrate density was driven by concentrations of dissolved carbon and nutrients supporting stream food webs. Dolly Varden abundance was primarily related to water temperature with fewer fish in warmer streams, whereas Dolly Varden energy density decreased with the flashiness of the headwater streams. Dolly Varden biomass was related to both temperature and bottom-up food web effects. The energy density of Arctic Grayling decreased with warmer temperatures and discharge flashiness. These relations demonstrate the importance of terrestrial–aquatic connections in permafrost landscapes and indicate the complexity of landscape effects on fish. Because permafrost thaw is one of the most impactful changes occurring as the Arctic warms, an improved understanding of how stream temperature, hydrology, and bottom-up food web processes influence fish populations can aid forecasting of future conditions across the Arctic.

KEYWORDS
Arctic grayling, dissolved organic carbon, dissolved organic nitrogen, Dolly Varden, flashiness, food webs, headwater streams, permafrost, water temperature

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INTRODUCTION

Climate change is impacting freshwater ecosystems worldwide with unprecedented changes observed in Arctic and Subarctic regions (Hinzman et al., 2005; Rantanen et al., 2022). One of the most ubiquitous changes occurring from climate warming in Arctic ecosystems is permafrost thaw (Smith et al., 2002). Permafrost is ground that remains frozen year-round and is common in cold high-latitude environments such as Alaska. Permafrost thaw increases infiltration potential and subsurface hydrologic flow, which in turn may alter catchment-stream interactions, and subsequently the chemistry, temperature, and timing of inflows to streams (Koch et al., 2024; Koch, Bogard, et al., 2022; Toohey et al., 2016; Walvoord et al., 2012). By modifying the hydrology, temperature, and water quality of freshwater lotic systems, thawing permafrost may have biological consequences. The biological responses to the rapidly changing stream hydrology and chemistry are difficult to predict due to the complex linkage between physical and ecological responses to permafrost thaw (Jorgenson et al., 2013; O'Donnell et al., 2020). Examining fish responses across watersheds with different permafrost characteristics provides insights into the biological links between permafrost and lotic food webs. Moreover, gradients of permafrost characteristics, such as decreases in permafrost extent, reflect future stream conditions that are expected to have ecological effects (Tank et al., 2020).

Permafrost characteristics govern multiple mechanisms that influence fish in Arctic streams by controlling the connectivity between terrestrial landscapes and streams (Murdoch et al., 2021; Myrstener et al., 2021). Foremost, permafrost limits infiltration, thereby controlling the magnitude and timing of stream inflows (Walvoord et al., 2012). For instance, permafrost landscapes with more infiltration and deeper flow paths allow infiltrating water to bypass headwater streams (McKenzie & Voss, 2013), leading to low-order streams that have less baseflow and greater discharge variability (Koch, Sjöberg, et al., 2022). Discharge affects multiple life history stages of fish by altering habitat suitability and physiological demands (Freeman et al., 2022; Humphries et al., 2020; Marsh et al., 2022). Floods during the egg-incubation period can scour streambeds, leading to in-gravel egg mortality (Honea et al., 2016) or contribute to sediment deposition (Jensen et al., 2009). Discharge can influence fish, particularly juveniles, as water velocity impacts drift feeding success (Bozeman & Grossman, 2019; Marsh et al., 2022; Naman et al., 2018) and directly alters the prey base for fish (Patrick & Yuan, 2017). Low discharge can create unsuitable water levels during the summer rearing period, change the timing of seasonal movements, and reduce juvenile production (Honea et al., 2016; Ohlberger et al., 2018). Ultimately, low discharge events can create ecosystem contraction (Doering et al., 2007; Jaeger et al., 2014; Stanley et al., 1997; Ward et al., 2020) and we suspect the loss of headwater habitat could be particularly influential on Arctic Grayling (*Thymallus arcticus*) that disperse throughout a watershed by size, with larger fish occurring in headwaters to benefit from more optimal, colder summer temperatures (Heim et al., 2019; Hughes, 1999). Loss of connectivity also affects fish by limiting access to preferred rearing habitat (Sethi et al., 2022).

Water temperature and the chemical composition of surface water are driven in part by permafrost altering subsurface flow paths that connect ground water to surface water. By limiting infiltration, permafrost can result in warmer summer groundwater because shallow runoff is moving through warm, shallow soils in contrast to deeper, colder flow paths that can reduce inflow and headwater stream temperatures (Sjöberg et al., 2021). Water temperature is a main factor directly governing the biology of fish and ultimately determining their production and survival in both lotic and lentic systems (Carey & Zimmerman, 2014; Magnuson et al., 1990; Sharma et al., 2007). By affecting the subsurface flow paths, permafrost also influences the transport and cycling of carbon, major nutrients (nitrogen, phosphorus), base cations, and other elements as they move through soils to streams (Frey & McClelland, 2009; Vonk et al., 2015). Thaw depth, or the depth from the surface to frozen ground, is a key determinant of whether lateral flow paths are routed through shallow organic soils or deeper mineral soils controlling the timing and amount of carbon and nutrients entering aquatic ecosystems (O'Donnell et al., 2016). By changing nutrient quantity and carbon quality, along with the timing that these nutrients and carbon are available, permafrost influences autochthonous production (Myrstener et al., 2021; Robbins et al., 2020). For example, Arctic streams have been shown to respond to experimental manipulations of nutrients with rapid biological uptake of nitrogen (Edwardson et al., 2003; Koch et al., 2013), phosphorus (Benstead et al., 2005; Peterson et al., 1993), and carbon (King et al., 2012; Warren et al., 1964). Moreover, additions of limiting nutrients have been shown to promote bottom-up effects on the entire ecosystem including invertebrates and fish in many systems (Bernhardt & Likens, 2002; Mejia et al., 2016; Warren et al., 1964), and also in Alaska (King et al., 2012; Peterson et al., 1993; Robbins et al., 2020). Understanding changes in thermal regimes and the bottom-up effects on fish governed by permafrost characteristics provides insights into factors

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structuring aquatic food webs in Arctic streams and aids in prediction for when permafrost thaws.

To address uncertainties in the relation between permafrost characteristics and fish performance, we explored linkages between hydrologic and biogeochemical factors with the abundance, biomass, and energy density of juvenile Dolly Varden (*Salvelinus malma*) and Arctic Grayling (*T. arcticus*) in headwater streams of Arctic watersheds (Figure 1). We focus on headwater streams due to their proximal lateral connection with the terrestrial landscape, making permafrost characteristics a major determinant of headwater stream hydrology and biogeochemistry (Koch, Sjöberg, et al., 2022). Headwater streams are also important for spawning and rearing fish and yet are understudied in permafrost landscapes (Callahan et al., 2015; Vonk et al., 2015). Comparing Dolly Varden and Arctic Grayling offers a useful contrast for assessing the influence of different hydrological and chemical factors. Arctic Grayling are residents that primarily forage on drifting insects and are tolerant of a range of water quality conditions (Bozeman & Grossman, 2019; Davis et al., 2019; McFarland et al., 2018), whereas Dolly Varden are amphidromous or residents (Carey et al., 2021), with juveniles foraging on benthic invertebrates. Furthermore, there is a lack of information on these species in Arctic ecosystems (Ellenor et al., 2022). We implemented a comparative design across watersheds with different ice content, soil texture, aspect, and ground temperature that results in tributaries with different near-stream and near-surface permafrost extent, infiltration, and depth of subsurface flow paths. With this design, we compare permafrost extent to water temperature, discharge flashiness (an index of streamflow variability; Baker et al., 2004), carbon and nutrient concentrations, and subsequent changes in biofilm and macroinvertebrates to Dolly Varden and Arctic Grayling abundance, biomass, and energy density in headwater tributaries of Arctic rivers.

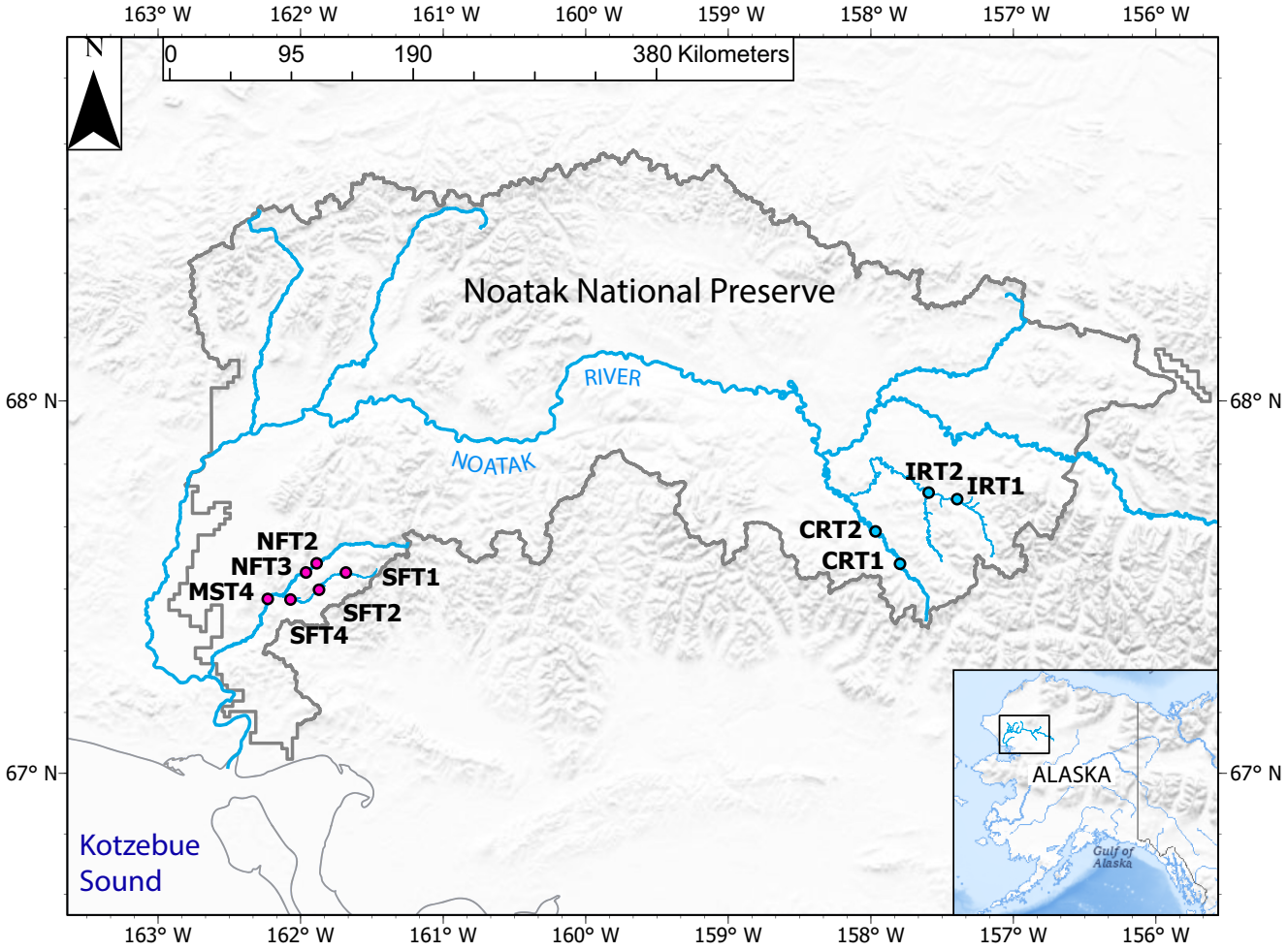


FIGURE 1 Location of headwater streams in the Noatak National Preserve (Table 1). Headwater streams are identified within larger river catchments of the Agashashok (MST4, NFT2, NFT3, SFT1, SFT2, and SFT4), Cutler (CRT1, CRT2), and Imelyak (IRT1, IRT2), rivers. Ice-poor watershed in red and ice-rich watershed in blue.

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METHODS

Study region

The study was conducted in the western Brooks Range of Alaska in Noatak National Preserve, focusing on headwater catchments in the Agashashok River, Cutler River, and Imelyak River basins (Figure 1). The Agashashok River drains the Baird Mountains with valleys containing fine-grained glacio-fluvial sediments overlying coarser cobbles. In the Cutler and Imelyak watersheds, surficial geology is characterized by glaciolacustrine sediments (Hamilton, 2001; O'Donnell et al., 2016). Tundra is the dominating vegetation type along streams in the Cutler and Imelyak watersheds and the north-facing tributaries of the Agashashok River, while forest cover (white spruce, *Picea glauca*) is commonly found along the south-facing streams in the Agashashok catchment (Sjöberg et al., 2021). The slopes along the study streams in the Cutler and Imelyak watersheds are underlain by ice wedges as evidenced by polygonal ground indicating the presence of ice-rich permafrost. By contrast, the slopes along the Agashashok headwater streams are largely free of landforms and terrain indicative of ice-rich permafrost (Sjöberg et al., 2021). Variability in permafrost characteristics across watersheds allows comparisons among catchments varying in hydrology and biogeochemistry.

Limited information exists on the fish community in the headwater streams of the study watersheds (ADF&G Alaska Freshwater Fish Inventory, 2024, www.adfg.alaska.gov). The species composition of resident fish is dominated by Sculpin (Cottidae), Dolly Varden, and Arctic Grayling. Other freshwater species in the region include Round Whitefish (*Prosopium cylindraceum*), Longnose Sucker (*Catostomus catostomus*), Humpback Whitefish (*Coregonus clupeaformis*), Northern Pike (*Esox lucius*), and Burbot (*Lota lota*). Potential diadromous species are Coho Salmon (*Oncorhynchus kisutch*), Chum Salmon (*Oncorhynchus keta*), Pink Salmon (*Oncorhynchus gorbuscha*), Sockeye Salmon (*Oncorhynchus nerka*), and Inconnu (*Stenodus leucichthys*; Schwanke & Johnson, 2016).

Study design

Using permafrost characteristics, we evaluated the interactive effects of ice-rich (Cutler and Imelyak) and ice-poor (Agashashok) catchments with a gradient of near-stream and near-surface permafrost extent (Figure 1; Table 1) on stream ecosystems. Within each watershed, we label the individual tributaries with a code that identifies the watershed and the location of the tributary within the watershed with a lower number closer to the headwaters (e.g., Cutler River highest elevation tributary is CRT1; Figure 1). We used estimates of near-stream (within 1000 m of the stream) and near-surface permafrost (the fraction of watershed area where permafrost, or active layer thickness, is <1 m from the ground surface) following Jorgenson et al. (2009) and Sjöberg et al. (2021). The extent of near-stream and near-surface permafrost (henceforth "permafrost extent") is a useful proxy for the impact of permafrost on hydrology and subsequently stream temperature, discharge, and biogeochemistry (Koch, Sjöberg, et al., 2022; Sjöberg et al., 2021). Permafrost extent ranged between 24.8% and 71.8% across headwater catchments (Table 1). We consider ice-poor and ice-rich watersheds, as prior work has shown that higher ground ice content increases stream dissolved organic carbon (DOC) concentration, reduces DOC age, and alters dissolved organic matter composition (O'Donnell et al., 2016, 2020). Within the ice-rich versus ice-poor landscapes are mainstem rivers that fork to form separate watersheds, and nested within each fork of the mainstem river are headwater tributaries of different size, elevation, and permafrost extent. The experimental units for our study design are: North fork Agashashok River ($n = 3$), South fork Agashashok River ($n = 3$), Imelyak River ($n = 2$), and Cutler River basins ($n = 2$) (Figure 1; Table 1).

Headwater food webs

Fish were collected in August and early September from 2016 to 2018 (Table 1) using minnow traps and single-pass backpack electrofishing (Reynolds & Kolz, 2013). Upon capture, fish were identified to the species level, and then Dolly Varden and Arctic Grayling were killed and frozen for shipment back to the laboratory (Carey, Koch, et al., 2023). Fish length (in millimeters) was measured in the laboratory, and fish biomass was calculated with length-mass relations for Arctic Grayling (Carlander, 1969; Froese & Pauly, 2023; Huo et al., 2011; Zhang et al., 2016) and Dolly Varden (Jones & Faurot, 1991). Catch per unit effort (CPUE) for fish abundance and biomass was calculated as the number or biomass of fish divided by electrofishing time or soaking time for minnow traps each year and then averaged across years for each tributary. Minnow traps were used to solely assess Dolly Varden as minnow traps are inefficient at capturing Arctic Grayling. Next, we assessed somatic tissue energy density using bomb calorimetry (Carey, Reeves, et al., 2023; Farley et al., 2011). Dorsal muscle plugs of Arctic Grayling and Dolly Varden were collected and placed in a freeze dryer (VirTis, Freezemobile 12) at—50°C for 48 h, homogenized with a

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TABLE 1 Average values and SDs of watershed size, elevation, average watershed aspect, permafrost characteristics, physical parameters, and water quality in each headwater stream[a] from 2016 to 2018.

	Ice-rich				Ice-poor					
Characteristic	**CRT1**	**CRT2**	**IRT1**	**IRT2**	**MST4**	**NFT2**	**NFT3**	**SFT1**	**SFT2**	**SFT4**
Area (km^2)	3.4	41.4	1.4	73.5	8.6	13.7	9.0	12.3	25.9	32.6
Elevation (m)	411	470	525	618	299	419	353	516	397	252
Aspect (°)	41	194	209	186	137	171	197	349	322	341
PF (%)	67.1	71.8	65.9	64.0	24.8	46.1	36.6	30.8	57.4	78.9
Temp (°C)	10.34	11.20	11.25	11.63	7.98	8.55	9.26	8.17	9.69	11.00
SD	1.23	0.53	0.03	0.49	1.02		0.92	0.60		0.72
Flash	0.66	0.97	0.16	0.31	0.33	0.17	0.37	0.20	0.30	0.48
DOC (mg C L^{-1})	6.88	5.83	4.05	6.10	1.38	2.37	2.98	0.68	1.65	4.70
SD	1.36	2.14	0.88	1.41	0.46	0.50	0.84	0.20	0.54	1.56
DIC (mg C L^{-1})	25.28	37.38	44.30	39.93	34.89	54.61	52.94	38.03	42.21	47.76
SD	12.66	6.12	0.90	2.50	3.63	5.33	3.27	1.37	2.60	2.64
DON (mg N L^{-1})	0.20	0.26	0.32	0.31	0.27	0.20	0.12	0.20	0.22	0.21
SD	0.01	0.06	0.17	0.07	0.05	0.10	0.03	0.06	0.04	0.13
NO_3^-:NO_4 (mg N L^{-1})	0.001	0.025	0.076	0.036	0.110	0.050	0.009	0.078	0.065	0.045
SD	0.001	0.013	0.073	0.034	0.024	0.041	0.010	0.024	0.008	0.021
TDP[b] (mg P L^{-1})	0.003	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
SD	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PO_4^{3-}[b] (mg P L^{-1})	0.0015	0.0015	0.0015	0.0013	0.0010	0.0010	0.0012	0.0005	0.0010	0.0010
SD	0.0006	0.0006	0.0013	0.0010	0.0011	0.0010	0.0016	0.0000	0.0014	0.0014

Note: The SD is provided where possible.

Abbreviations: Area, watershed area; aspect, mean aspect of watershed; DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; elevation, mean elevation of watershed; flash, discharge flashiness; NO_3^-:NO_4, nitrate-nitrite; PF, permafrost extent; PO_4^{3-}, phosphate; TDP, total dissolved phosphorus; temp, temperature.

[a]Headwater stream see Figure 1.

[b]If TDP or PO_4^{3-} was below the detection limit of 0.002 mg P L^{-1} for TDP and 0.001 mg P L^{-1} for PO_4^{3-}, the value was set to half the detection limit (Antweiler & Taylor, 2008).

mortar and pestle, and a ≤150 mg pellet was pressed from a subsample and weighed immediately. A semimicro Parr 1425 calorimeter was used to measure somatic energy following the Parr manual (Parr Instrument Company 1994). Benzoic acid was used as the standard as per manufacturer, and duplicate tissue samples were used to evaluate the instrument precision. Somatic energy from the calorimeter (in calories per gram of dry mass) was converted to kilojoules and reported per unit dry mass (in kilojoules per gram of dry mass). Energy density was determined for fish in 2016 and 2017. For each headwater stream, energy density was averaged independently for Arctic Grayling and Dolly Varden and then averaged between years. Dolly Varden captured by minnow traps were included in the analysis of energy density.

Benthic biofilm and benthic macroinvertebrates were examined in late summer (2016–2018). Benthic biofilm was measured in situ using a Benthotorch (bbe Moldaenke, Kiel, Germany) hand-held fluorometer, which distinguishes taxa (green algae, cyanobacteria, diatoms) and provides estimates of standing biomass. Each tributary was measured at three random transects, and at each transect, three measurements were taken with the Benthotorch near the right bank, in the middle of the thalweg, and near the left bank. The nine biofilm measurements were averaged to characterize the headwater tributary each year and then averaged across years. Benthic macroinvertebrates were sampled using kick nets. For each headwater stream, four kick net samples were collected in riffles and four kick net samples were collected in runs, with collections lasting 1 min per sample and encompassing 0.4-m^2 area. In the laboratory, individual macroinvertebrates were identified to the lowest practical taxonomic level (usually Family) to compare composition, richness, and density. Macroinvertebrate samples were processed by the National Aquatic Monitoring Center (Logan, UT, USA; Carey

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et al., 2024). To compare macroinvertebrates, we focused on taxa richness (number of unique taxa standardized to operational taxonomic units) and total density (estimated number of individuals per unit area square meter; Ludwig & Reynolds, 1988; Merritt et al., 2008).

Water temperature

Temperature loggers were deployed in early June and retrieved in late August or early September in 2017 and 2018 (Carey et al., 2020; Koch et al., 2019). Temperature was recorded every 15 min using Tidbit v2 (±0.21°C), HOBO Water Temp Pro v2 (Onset Computer Corporation 2013; Bourne, MA, USA) and In Situ (Fort Collins, CO, USA) pressure transducers (Rugged Troll 100 s [accuracy ±0.3°C] and Level Troll 500 and 700 s [accuracy ±0.1°C]). Multiple loggers were secured in the thalweg of each headwater stream within ~50 m of the confluence with the mainstem and ~200 m upriver from the mainstem confluence. In the streams, temperature loggers were secured to the bottom using duckbill anchors and shielded from solar radiation (Mauger et al., 2015). Pressure transducers were secured to rebar. We assumed the stream water was well mixed and took point measurements of temperature with a YSI Professional Plus multiparameter meter (YSI, Yellow Springs, OH) for comparison to the continuous loggers during instrument installation and retrieval. Temperature data quality was assessed by comparing diurnal patterns and relations between loggers in the same headwater stream. The seven-day average daily maximum (7-DADMax) temperature (in degrees Celsius) was calculated across the deployed logger duration during the open-water season for each tributary in 2017 and 2018. The 7-DADMax for an individual day is calculated by averaging that day's daily maximum temperature with the daily maximum temperatures of the three days prior and the three days after that date (ADEC, 2024). The 7-DADMax measurements were averaged each year and then the annual means were averaged for each tributary for the analysis.

Water quantity

We monitored continuous stream discharge in the headwater streams (Koch et al., 2019). Stream stage was measured at the mouth of all streams at 15-min intervals between early June and mid-September using vented pressure transducers (In Situ Inc., Level Logger 500 or 700 s) or absolute pressure transducers (In Situ, Rugged Troll 100 s) corrected for barometric pressure. Discharge was measured during site visits in the early and late summer using a wading rod and either a mechanical meter, Flowtracker 1, or Flowtracker 2 acoustic velocity profiler (Sontek, San Diego, CA, USA). Rating curves were developed between stage and discharge measurements and used to calculate continuous discharge. More details can be found in Koch, Sjöberg, et al. (2022). In 2017, flashiness was calculated for tributaries by dividing the sum of the absolute values of day-to-day changes in mean daily flow by total discharge during a specified time interval and can range between zero and one (Baker et al., 2004). Using flashiness standardizes across stream size, and larger values indicate more flashy streams.

Water quality

Water samples were collected at the end of the open-water periods in August and September in 2016–2018 (O'Donnell et al., 2021). In 2016, two samples separated by ~3 weeks were collected in tributaries MST4, NFT2, SFT1, SFT2, and SFT4 (Figure 1) and averaged for the below analysis. Samples were collected for measurement of DOC concentration and nutrients (N, P) using a 0.45-μm high-capacity capsule filter connected to a Geopump Series II Peristaltic Pump (Geotech Environmental Equipment, Denver, CO). DOC concentrations were determined using an O.I. Analytical Model 700 TOC analyzer via the platinum catalyzed persulfate wet oxidation method (Aiken, 1992). All nitrogen species concentrations were measured on a Lachat Quikchem 8500 (Hach Company, Loveland, CO, USA). Total dissolved nitrogen (TDN) was determined using the persulfate digest method, unionized ammonia (NH_3) was determined using the Salicylate method, and the sum of nitrate and nitrite ($NO_3^- + NO_2^-$; henceforth only referred to as NO_3^-, as NO_2^- comprises a negligible fraction of the sum) was determined by cadmium reduction. DOC and nutrient samples were averaged across years for each tributary. We focus on DOC, dissolved inorganic carbon (DIC), dissolved organic nitrogen (DON), NO_3^-, total dissolved phosphorous (TDP), and phosphate (PO_4^{3-}) as measures of productivity (O'Donnell et al., 2010) and combine them into one factor (henceforth WQ1) using principal components for the analysis. The data were standardized (mean = 0 ± 1 SD) in a correlation matrix before running the principal components analysis.

Analysis

To examine the influence of permafrost characteristics on fish, we evaluated relations between permafrost extent and the abundance, biomass, and energy density of Arctic Grayling and Dolly Varden using linear regression.

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For subsequent analyses, we focused on Dolly Varden caught by electrofishing because estimates of abundance and biomass from electrofishing and minnow traps had a similar linear relation with permafrost extent. Next, to examine the factors driving the influence of permafrost extent on fish responses, we confirmed relations between permafrost extent and temperature, flashiness, or WQ1 using linear regression and included ice-rich versus ice-poor watersheds as a factor. We explored the relation of WQ1 in supporting the stream food web by comparing WQ1 to phytobenthic biomass and subsequently phytobenthic biomass to the abundance of macroinvertebrates using linear regression. We combined cyanobacteria, diatoms, and green algae to calculate phytobenthic biomass by summing the taxon-specific biomasses measured by the fluorometer. Phytobenthic biomass represents the primary production in the tributaries and energy flow from the base of the food web. We used macroinvertebrate abundance as an indicator of prey resources for fish across headwater food webs.

We assessed the relative importance of temperature, flashiness, and macroinvertebrate density on fish responses using Akaike information criterion (small sample size correction, AIC_c). We selected these variables because they are primary drivers linking landscape changes to aquatic ecosystems in headwater streams of Arctic watersheds (Koch, Sjöberg, et al., 2022; O'Donnell et al., 2020; Sjöberg et al., 2021). AIC_c is a maximum likelihood estimate of the Kullback–Leibler information criteria with which estimation and model selection can be combined under the framework of optimization (Burnham & Anderson, 1998). We examine all combinations of temperature, flashiness, and macroinvertebrate density in models predicting fish responses and then compare model strength among the alternative models. Models were separately tested for Arctic Grayling and Dolly Varden abundance, biomass, and energy density. For all models, the variance inflation factor was assessed for multicollinearity (Myrvold & Kennedy, 2015; Nelson et al., 2015). We report the number of variables, AIC, AIC_c, δAIC_c, and weight (relative likelihood of each model) for each model and focus on models within 2 δAIC_c units. Models within 2 δAIC_c were considered equally well supported in predicting the fish responses (Burnham & Anderson, 1998). Finally, we compared the key regressors identified by the AIC_c analyses to the abundance, biomass, and energy density of Arctic Grayling and Dolly Varden.

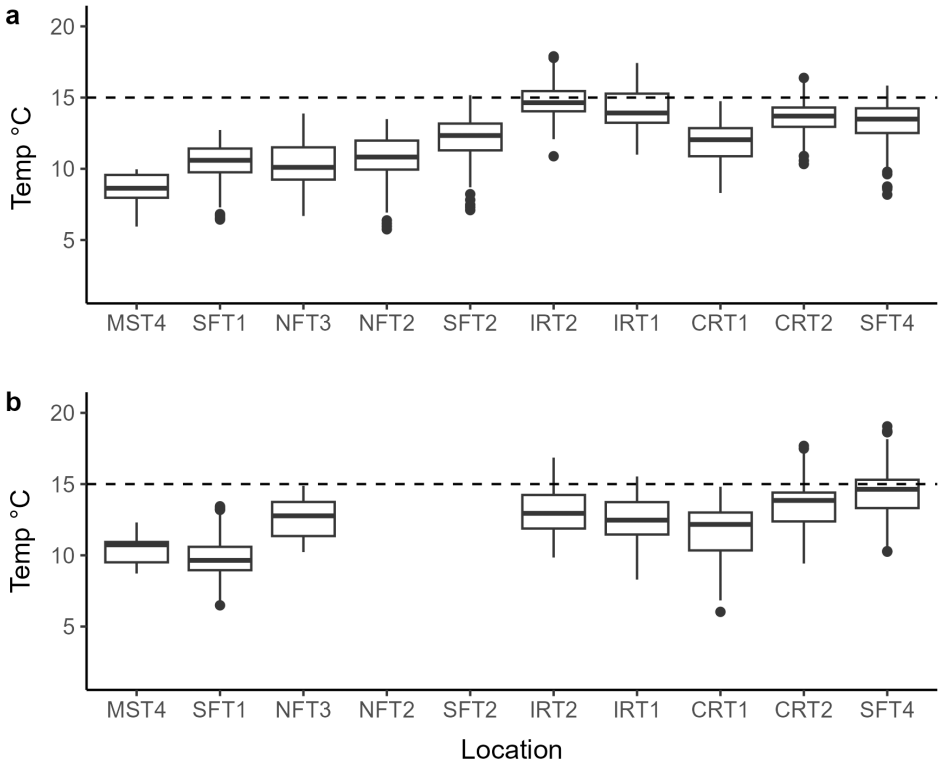


FIGURE 2 Boxplots of seven-day average daily maximum (7-DADMax) temperature (in degrees Celsius) plotted for each stream in the (a) 2017 and (b) 2018 open-water season. The 7-DADMax for an individual day is calculated by averaging that day's daily maximum temperature with the daily maximum temperatures of the three days prior and the three days after that date. The lines within boxes are the medians, boxes encompass the 25th and 75th percentiles, and whiskers are the 1.5× interquartile ranges. The streams are arranged by increasing permafrost extent. The dashed line indicates 15°C, the temperature that is the EPA guidance mark for water temperature in Alaska (ADEC 2024).

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All analyses were performed using R Statistical Software (v4.3.2; R Core Team, 2023). The principal components analysis on water quality data was conducted with the "prcomp" function in the "stats" package in R (R Core Team, 2023). The linear regression analyses were also conducted with the "stats" package in R using the "lm" function (R Core Team, 2023). The AIC_c analyses comparing models to fish responses used the "AICmodavg" package (Mazerolle, 2023).

RESULTS

Physical and chemical parameters

Stream water temperatures, discharge flashiness, and carbon and nutrients varied across headwater catchments with different permafrost characteristics (Table 1). The mean annual temperature of the headwater streams in 2017 and 2018 ranged between 7.9 and 11.6°C (Table 1). Within years, stream water temperature varied through the open-water season and across tributaries with different permafrost extents. Average daily temperatures ranged between 3.7 and 17.4°C in 2017 and 2.4 and 15.9°C in 2018 across streams. The 7-DADmax values exceeded 15°C (the water temperature criteria not to be exceed for rearing and migrating salmon in Alaska waters, ADEC, 2024) in multiple locations in both 2017 and 2018 (Figure 2). The 7-DADmax exceeded 15°C in the ice-rich CRT2 (9 days in 2017, 11 days in 2018), IRT1 (18 days in 2017, 8 days in 2018), and IRT2 (22 days in 2017, 9 days in 2018), along with the high permafrost extent tributaries of SFT4 (10 days in 2017, 23 days in 2018) and SFT2 (4 days in 2017). Variation in total and average daily discharge during the open-water season resulted in differences in flashiness that ranged between 0.16 and 0.97 across headwater streams (Table 1). Flashiness was more variable among headwater streams in catchments with higher ice content (Figure 3).

The concentrations of dissolved carbon, nitrogen, and phosphorus confirmed the oligotrophic status of the headwater streams. The highest concentrations for each component were DOC 6.8 mg C L^{-1}, DIC 54.6 mg C L^{-1}, DON 0.32 mg N L^{-1}, and nitrate-nitrite 0.11 mg N L^{-1} (Table 1). TDP ranged between the detection limit and 0.0027 mg P L^{-1} and PO_4^{3-} ranged between the detection limit and 0.0017 mg P L^{-1} (Table 1). The principal components analysis combining carbon (DOC and DIC), nitrogen (DON and NO_3–), and phosphorus (TDP and PO_4^{3-}) found the first principal component (WQ1) explained 50.9% of the variation, while principal component two (PC2) explained 24.9% and principal component three explained 16.4% of the variation. The biplot of WQ1 and PC2 demonstrates DOC, PO_4^{3-}, and TDP had similar loadings, as the vectors pointed in matching directions indicating headwater streams with lower WQ1 scores had higher amounts of DOC, PO_4^{3-}, and TDP (Figure 4). The magnitude of DOC, however, was greater than PO_4^{3-} and TDP as indicated by the length of the vector. DIC and DON were of a similar magnitude, but loadings were in opposite directions. Headwater streams with higher PC2 values had lower DIC and higher DON concentrations. The vector of NO_3^- had a similar magnitude to DOC, DIC, and DON, but a separate direction in the PCA biplot (Figure 4).

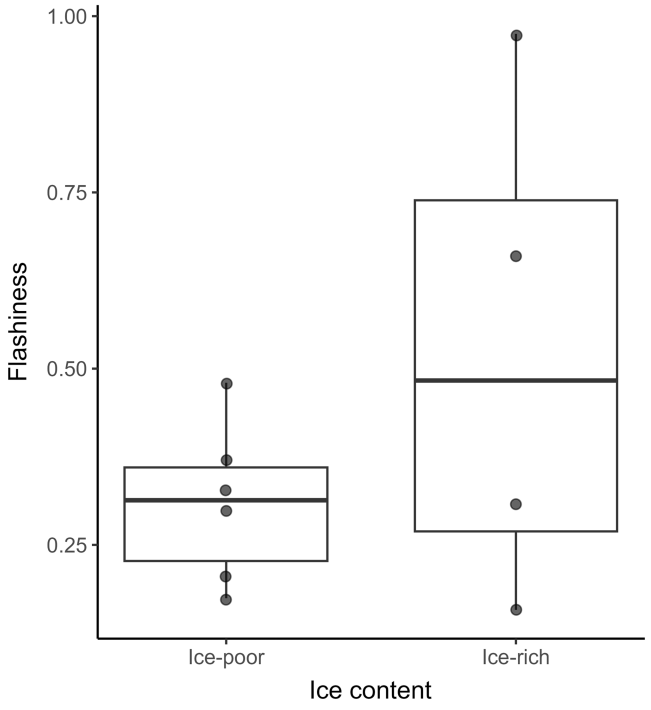


FIGURE 3 Boxplots of flashiness for each headwater stream comparing ice-poor and ice-rich catchments. Flashiness is unitless and calculated by dividing the sum of the absolute values of day-to-day changes in mean daily flow by total discharge during the study period (Baker et al., 2004). The lines within boxes are the medians, boxes encompass the 25th and 75th percentiles, and whiskers are the 1.5× interquartile ranges.

We observed relations between permafrost characteristics and the physical and chemical parameters of headwater streams. Headwater streams with greater permafrost extent had warmer stream temperatures (adj. $r^2 = 0.74$; $p = 0.004$; Figure 5a). The relation between permafrost extent and stream flashiness was not significant (adj. $r^2 = 0.06$; $p = 0.33$; Figure 5b); however, a significant interaction was found in the regression model between the ice-poor versus ice-rich factor and permafrost extent (ice-rich vs. ice-poor × permafrost; $p = 0.01$). The interaction stems from the different slopes of the lines for ice-rich and ice-poor watersheds with a larger

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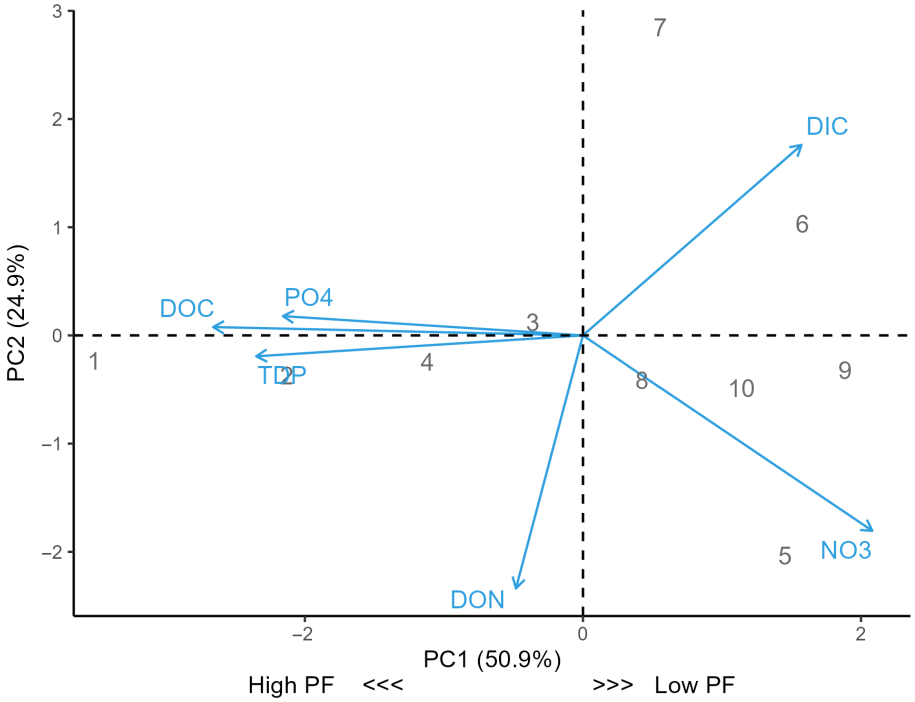


FIGURE 4 Results of principal components analysis on water quality parameters. Parameters include concentrations of carbon (dissolved organic carbon [DOC] and dissolved inorganic carbon [DIC]) and nutrients (dissolved organic nitrogen [DON] nitrate and nitrite [NO_3^-], total dissolved phosphorus [TDP], and phosphate [PO_4^{3-}]) in headwater streams indicated by numbers in figure. Principal component 1 (WQ1 in text) is plotted with principal component 2 (PC2). The direction of each component is indicated by the blue arrow and the length of the arrow represents the magnitude of the component. The relation of PC1 to permafrost (PF) extent is indicated on the plot.

regression coefficient in the ice-rich streams; however, neither factor by itself was significantly related to permafrost extent. Headwater streams in catchments with lower permafrost extent had higher values of C, N, and P, and there was a significant relation between permafrost extent and WQ1 ($r^2 = 0.79$; $p = 0.004$; Figure 5c).

Biological parameters

Food web components varied across the headwater catchments with different permafrost extents and ice content. In the ice-poor watersheds, phytobenthic biomass was higher in the south-facing streams (MST4, NFT3, and NFT2) compared with the north-facing streams (SFT1, SFT2, and SFT4; Figure 6). Diatoms dominated the biofilm in the ice-poor watersheds with variation in the density of green algae and cyanobacteria (Figure 6). Phytobenthic biomass in streams of ice-rich watersheds had a similar range to the ice-poor streams, but was more evenly mixed across diatoms, green algae, and cyanobacteria (Figure 6). Macroinvertebrate richness ranged from 6 to 19 taxa across years, and assemblages were dominated by the families Chironomidae, Nemouridae, and Baetidae (Carey et al., 2024). Macroinvertebrate density ranged between 6.7 and 260.1 m^{-2} and was highest in a south-facing, ice-poor watershed (NFT2). The lowest macroinvertebrate density was observed in a north-facing, ice-poor watershed (SFT1; Carey et al., 2024).

Trophic levels were linked within the food webs of headwater streams and connected to the concentrations of carbon and nutrients. The concentrations of carbon, nitrogen, and phosphorus were related to phytobenthic biomass of the headwater streams. WQ1 had a negative relation with phytobenthic biomass, with less phytobenthic biomass found in streams with higher values of WQ1 grouped by ice content (adj. $r^2 = 0.33$; ice content $t = -2.54$, $p = 0.04$; WQ1 content $t = -2.18$, $p = 0.07$). Subsequently, phytobenthic biomass had a positive relation with macroinvertebrate density ($r^2 = 0.50$; $p = 0.02$), with greater macroinvertebrate densities in headwater streams with higher phytobenthic biomass. No relation was found between phytobenthic biomass and macroinvertebrate richness ($r^2 = 0.31$; $p = 0.098$).

Permafrost controls on fish

Regression analyses indicated a link between permafrost extent and fish abundance, biomass, and energy

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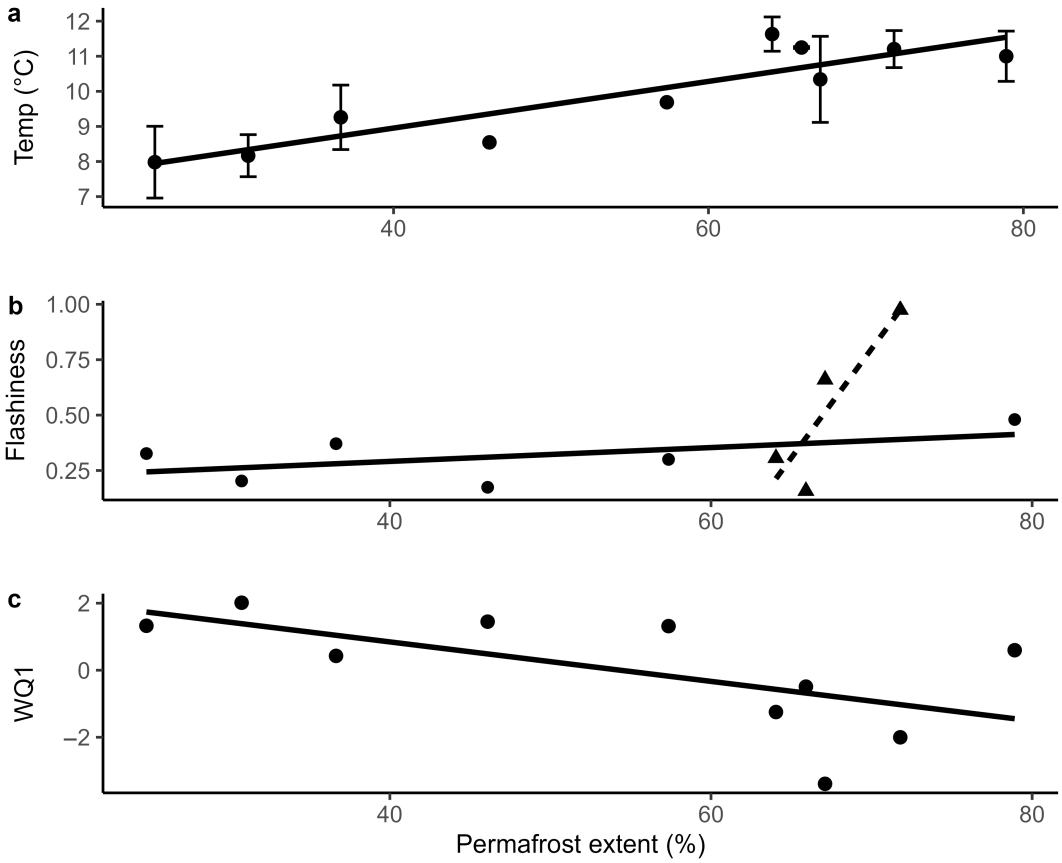


FIGURE 5 Plots between permafrost extent and (a) average temperature, (b) flashiness with ice-poor (circles) and ice-rich (triangles) plotted separately, and (c) the first principal component of the carbon and nutrient analysis (WQ1).

density (Figure 7). We observed negative relations between permafrost extent and Dolly Varden abundance captured from electrofishing ($r^2 = 0.92$; $p = <0.001$; Figure 7d) and minnow traps ($r^2 = 0.72$; $p = 0.002$; Figure 7g), as well as Dolly Varden biomass determined from fish collected with electrofishing ($r^2 = 0.59$; $p = 0.01$; Figure 7e) and minnow traps ($r^2 = 0.69$; $p = 0.003$; Figure 7h). We also documented a decreasing pattern between the energy density of Arctic Grayling and permafrost extent ($r^2 = 0.64$; $p = 0.005$) across headwater streams (Figure 7c). No relations were observed between Arctic Grayling abundance and biomass or Dolly Varden energy density with permafrost extent in headwater catchments.

Relative importance of abiotic and biotic factors

Different factors were identified as important determinants of Dolly Varden or Arctic Grayling abundance, biomass, and energy density by the AIC_c analyses. Dolly Varden abundance was evaluated with models that included all combinations of temperature, flashiness, and macroinvertebrate density. The top model used stream temperature in predicting Dolly Varden abundance estimated by electrofishing, as no other models were within two AIC_c units (Table 2). The temperature model was highly weighted (0.88) indicating its strength in predicting Dolly Varden abundance across headwater streams. For Dolly Varden biomass, two models were identified as strong models and highly weighted (Table 2). The first model contained temperature alone, similar to abundance, and the other model contained both temperature and macroinvertebrate density (Table 2). For Dolly Varden, abundance and biomass decreased with increasing temperature in the headwater streams (Figure 8a,b). There was not a strong individual relation between macroinvertebrate density and Dolly Varden biomass (Figure 8c). For Arctic Grayling, in contrast, no models predicted abundance or biomass (Table 3).

Highly weighted models were found for the energy density of both Dolly Varden and Arctic Grayling across headwater streams. The AIC_c analysis indicated a model with flashiness alone as the strongest model in predicting Dolly Varden energy density, with no other models

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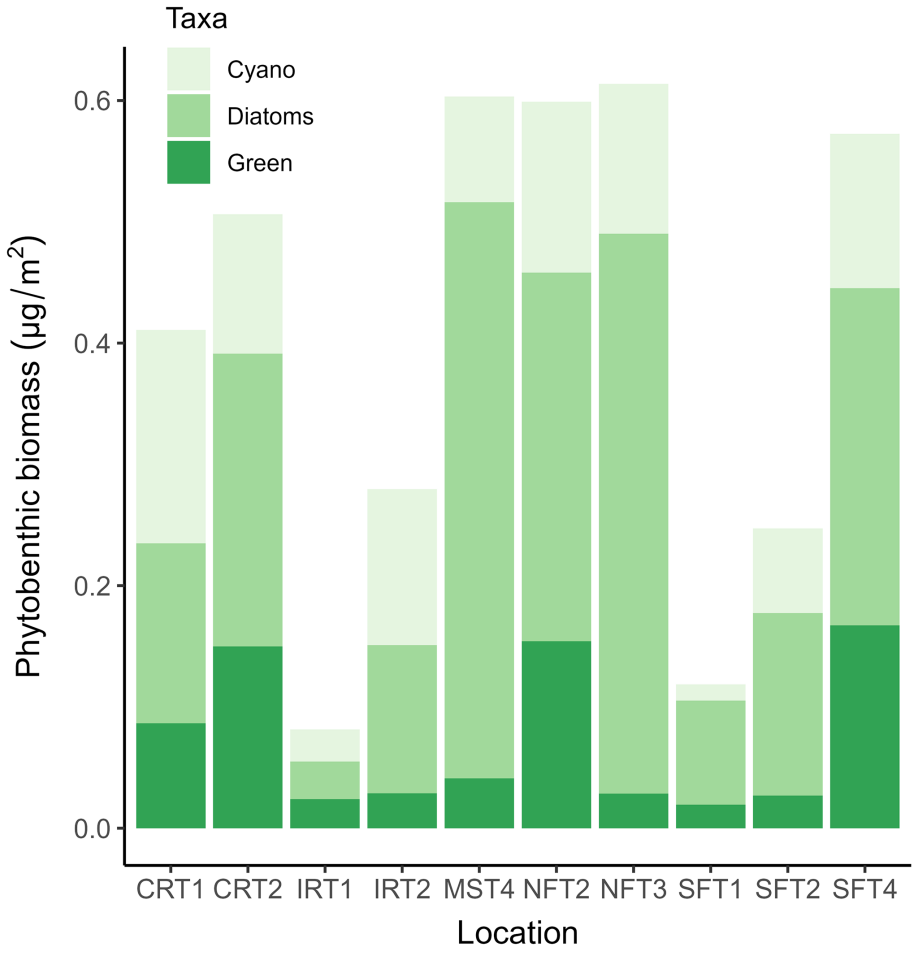


FIGURE 6 Stack bar chart of phytobenthic biomass across headwater streams. Phytobenthic biomass is divided into the amount of cyanobacteria (Cyano), diatoms, and green algae for each headwater stream. The headwater streams are from the Cutler River (CRT1 and CRT2), Imelyak River (IRT1 and IRT2), the south-facing North fork of the Agashashok River (MST4, NFT3, and NFT2), and north-facing South fork of the Agashashok River (SFT1, SFT2, and SFT4).

within two AIC_c units (Table 2; Figure 8d). Flashiness as a predictor of Dolly Varden energy density also had a high weight (0.78) compared with all other models considered in the analysis, confirming its importance. Models containing flashiness or flashiness and temperature were within two AIC_c units of each other, with similar weights suggesting both factors are predictive of the energy density of Arctic Grayling in headwater streams (Table 3; Figure 8g,h). The energy density of Arctic Grayling and Dolly Varden decreased with increasing flashiness in streams (Figure 8d,h).

DISCUSSION

Permafrost influences stream hydrology and water quality, thereby impacting fish that live in Arctic headwater streams. Both Dolly Varden abundance and biomass were lower in headwater streams within catchments with greater permafrost extent, and the pattern was consistent when using either electrofishing or minnow traps to assess the Dolly Varden responses. Energy density of Arctic Grayling was also related to permafrost, demonstrating decreasing energy density with increasing permafrost extent. Arctic Grayling abundance and biomass did not show a direct relation with the extent of permafrost, and no relation was observed between permafrost extent and Dolly Varden energy density. The different responses of Dolly Varden and Arctic Grayling indicate these fish species are being driven by different hydrological and biogeochemical factors, or a combination of factors, in headwater streams underlain by permafrost. Different responses between Dolly Varden and Arctic Grayling were expected due to their different life histories, optimal temperatures, and food web niches (Carrillo-Longoria et al., 2024; Takami et al., 1997). For instance, Dolly Varden has multiple life history strategies including amphidromous, partial migration, skip spawning, and

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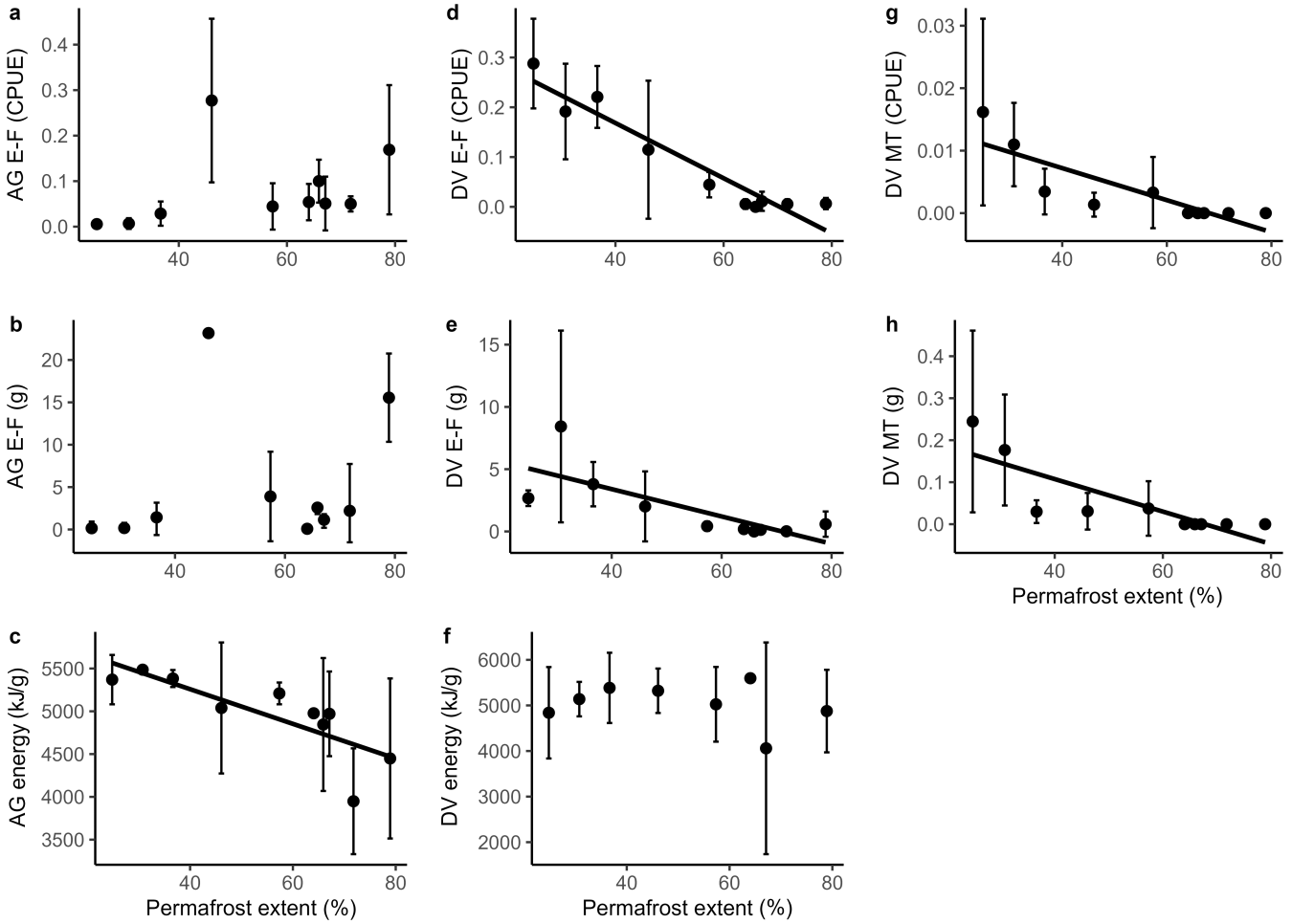


FIGURE 7 Relations between permafrost extent and fish responses (mean ± SD) of abundance, biomass, and energy density for Arctic Grayling (AG) and Dolly Varden (DV). AG (a) abundance (CPUE, catch per unit effort), (b) biomass, and (c) energy density were estimated by electrofishing (E-F). DV (d, g) abundance, (e, h) biomass, and (f) energy density were estimated by electrofishing and minnow traps (MT). A significant ($p < 0.05$) linear relation is indicated by the black line.

residents (Carey et al., 2021), whereas Arctic Grayling are widely distributed, freshwater residents (Hughes, 1999). Moreover, Arctic Grayling primarily forage on drifting insects and are more tolerant of a range of water quality conditions compared with juvenile Dolly Varden that forage mainly on benthic invertebrates.

Permafrost characteristics impact hydrologic and chemical factors in the headwater streams of our study area in northwest Alaska, United States of America (USA), (Koch, Sjöberg, et al., 2022; O'Donnell et al., 2016, 2020; Sjöberg et al., 2021; Figure 1); therefore, we expected to observe statistical relations between permafrost extent and water temperature, discharge, carbon, and nutrients. Near-surface permafrost limits infiltration and enhances shallow subsurface runoff through active layer soils (Carey & Woo, 2001; McNamara et al., 1998) governing the magnitude and timing of water reaching the stream along with influencing water quality (Koch et al., 2024). We observed the highest flashiness in an ice-rich catchment, which is consistent with previous findings of limited infiltration in our colder catchments containing more ice-rich permafrost (Koch, Sjöberg, et al., 2022). Overall, hydrographs were more variable in ice-rich catchments than ice-poor catchments. We also observed warmer stream water temperatures in headwater catchments with more permafrost, confirming prior observations and process-based model simulations from our study region (Sjöberg et al., 2021). Carbon and phosphorus in the surface water increased with more permafrost, confirming that shallow infiltration through organic soils results in higher amounts of carbon and nutrients being transported to the stream (MacLean et al., 1999; O'Donnell et al., 2016). Nitrogen was lower in headwater streams with more permafrost in the catchment, suggesting the complexity of terrestrial-aquatic linkages.

Permafrost-driven changes in hydrological and chemical factors were related to fish. We identified patterns between stream temperature, flashiness, and bottom-up

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TABLE 2 Analysis of predictors of Dolly Varden abundance, biomass, and energy density in headwater streams of Arctic watersheds.

Models	*K*	AIC_c	Delta_AIC_c	AIC_cWt	Cum.Wt	LL
DV CPUE						
T	3	−19.13	0	0.88	0.88	14.57
T + *M*	4	−13.57	5.56	0.05	0.93	14.79
T + *F*	4	−13.2	5.93	0.05	0.98	14.6
M	3	−11.35	7.78	0.02	0.99	10.68
F	3	−8.5	10.63	0	1	9.25
M + *F*	4	−6.56	12.57	0	1	11.28
All	5	−4.7	14.43	0	1	14.85
DV biomass						
T	3	51.44	0	0.51	0.51	−20.72
T + *M*	4	52.21	0.77	0.35	0.86	−18.11
F	3	55.37	3.92	0.07	0.93	−22.68
M	3	56.93	5.49	0.03	0.96	−23.46
T + *F*	4	57.02	5.58	0.03	0.99	−20.51
All	5	60.92	9.47	0	1	−17.96
M + *F*	4	61.32	9.88	0	1	−22.66
DV energy density						
F	3	124.59	0	0.78	0.78	−56.3
T + *F*	4	127.7	3.1	0.17	0.95	−53.2
M	3	131.75	7.15	0.02	0.97	−59.9
T	3	131.88	7.29	0.02	0.99	−59.9
M + *F*	4	133.05	8.46	0.01	1	−55.9
T + *M*	4	141.05	16.46	0	1	−59.9
All	5	146.12	21.53	0	1	−53.1

Abbreviations: AIC_c, Akaike information criterion corrected for small sample sizes; AIC_cCt, AIC_c cumulative model weight; AIC_cWt, AIC_c model weight; CPUE, catch per unit effort; DV, Dolly Varden; *F*, discharge flashiness; *K*, number of variables; LL, log likelihood; *T*, temperature (°C); *M*, macroinvertebrate density (in numbers per square meter).

effects through the food web on Dolly Varden and Arctic Grayling in headwater streams. Across headwater streams, temperature had a strong relation with Dolly Varden abundance and biomass and was an important factor for Arctic Grayling energy density. The importance of temperature is expected because temperature governs fish metabolism with energetic consequences (Magnuson et al., 1990); however, the direction of the relation is surprising as the warmer headwater streams had less Dolly Varden abundance and biomass and lower energy density of Arctic Grayling than cooler systems. We suspect these patterns are driven by differences in thermal optimum and what is bioenergetically suitable habitat for Dolly Varden (Bozeman & Grossman, 2019; Takami et al., 1997) and Arctic Grayling (Deegan et al., 1999; Haugen & Vollestad, 2000; LaPierrier & Carlson, 1973; Lohr et al., 1996; Marsh et al., 2022). Temperatures in the headwater streams with a higher permafrost extent exceeded optimal temperatures for Dolly Varden and Arctic Grayling, with temperature values often above 15°C and occasionally exceeding 18°C in some tributaries. This result questions whether food resources are sufficient to support the elevated metabolism of fish in warmer water and suggests cooler waters may be more bioenergetically favorable with lower feeding rates. Examining interannual variability in thermal regimes and the importance of terrestrial prey could help understand fish responses across permafrost landscapes.

Dolly Varden and Arctic Grayling showed decreasing energy density with increasing stream flashiness. The relation between flashiness and fish energy in our headwater streams suggests the flashier systems are likely harsher environments for both fish species. Flashiness reflects hydrologic extremes, with less flashy catchments dampening storm flow and lessening the impact on biotic communities. The flashiness of streams is important to

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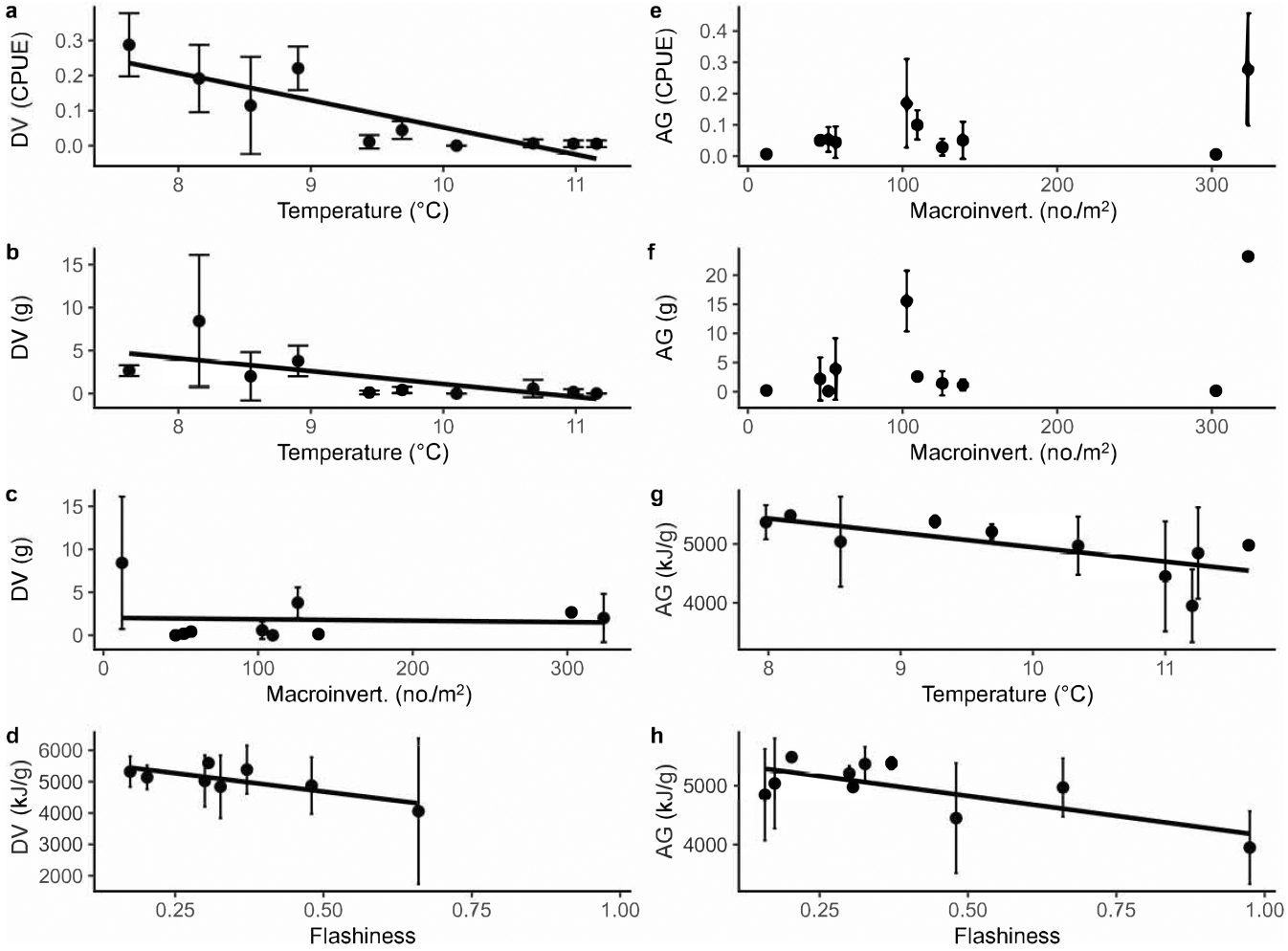


FIGURE 8 Linear regressions of abiotic and biotic factors identified as important to fish responses (mean ± SD) across headwater streams: (a) Dolly Varden (DV) abundance (CPUE, catch per unit effort) plotted with temperature; DV biomass plotted with (b) temperature and (c) macroinvertebrate density; (d) Dolly Varden energy density plotted with flashiness; (e, f) Arctic Grayling (AG) abundance and biomass plotted with macroinvertebrate density; AG energy density plotted with (g) temperature and (h) flashiness. A significant ($p < 0.05$) linear relation is indicated by the black line.

biotic communities as discharge can influence fish, particularly juveniles, as water velocity impacts drift feeding success (Bozeman & Grossman, 2019; Deegan et al., 1999; Naman et al., 2018). Higher discharge rates can be beneficial by increasing the number of encounters with prey for fish but can then cross a threshold in which swimming against high velocities becomes an energy cost (Deegan et al., 1999). We believe that our flashiness metric is predominantly indicating high flows rather than rapid drying. In some systems, flashiness also indicates the potential for rapid drying (Doering et al., 2007; Jaeger et al., 2014; Stanley et al., 1997; Ward et al., 2020), but this tends to be less true in the Arctic, where long recession curves are common due to the presence of large-saturated hillslope areas often characterized by water tracks (Koch et al., 2024; McNamara et al., 1998).

We did observe zero-flow days in two headwater streams over the course of the study (NFT2 and NFT3; Koch, Sjöberg, et al., 2022). While we suspect drying events are stressful to fish in the watershed, the headwater streams with zero-flow days had low flashiness in 2017 compared with other headwater streams and high energy density for both fish species. Drying events may also be lethal or result in fish moving to other habitats; however, we did not observe any relations between flashiness and fish abundance. More drying is expected in the future with thaw and vegetation encroachment (Koch, Sjöberg, et al., 2022). Increased zero-flow days could lead to the loss of fish habitat, which has also been observed in desert rivers of the Southwest United States (Doering et al., 2007; Jaeger et al., 2014; Stanley et al., 1997; Ward et al., 2020).

Differences in carbon and nutrients across permafrost characteristics influenced the standing biomass of

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TABLE 3 Analysis of predictors of Arctic Grayling abundance, biomass, and energy density in headwater streams of Arctic watersheds.

Model	*K*	AIC_c	Delta_AIC_c	AIC_cWt	Cum.Wt	LL
AG CPUE						
M	3	−12.68	0	0.33	0.33	11.3
F	3	−12.51	0.17	0.31	0.64	11.3
T	3	−12.33	0.34	0.28	0.92	11.2
T + *M*	4	−8.27	4.41	0.04	0.96	12.1
T + *F*	4	−7.19	5.48	0.02	0.98	11.6
M + *F*	4	−7.01	5.66	0.02	1	11.5
All	5	−0.74	11.93	0	1	12.9
AG biomass						
M	3	77.5	0	0.4	0.4	−33.8
F	3	78.2	0.69	0.28	0.69	−34.1
T	3	78.53	1.02	0.24	0.93	−34.3
T + *M*	4	82.59	5.09	0.03	0.96	−33.3
M + *F*	4	83.27	5.76	0.02	0.98	−33.6
T + *F*	4	84.05	6.55	0.02	1	−34.0
All	5	90.71	13.21	0	1	−32.9
AG energy density						
T + *F*	4	151.35	0	0.48	0.48	−67.7
F	3	152.79	1.44	0.24	0.72	−71.4
T	3	152.86	1.51	0.23	0.95	−71.4
T + *M*	4	157.72	6.36	0.02	0.97	−70.9
M + *F*	4	158.29	6.94	0.02	0.98	−71.2
All	5	158.94	7.59	0.01	0.99	−67.0
M	3	159.77	8.42	0.01	1	−74.9

Abbreviations: AG, Arctic Grayling; AIC_c, Akaike information criterion corrected for small sample sizes; AIC_cCt, AIC_c cumulative model weight; AIC_cWt, AIC_c model weight; CPUE, catch per unit effort; *F*, discharge flashiness; *K*, number of variables; LL, log likelihood; *M*, macroinvertebrate density (in numbers per square meter); *T*, temperature (in degrees Celsius).

biofilm in headwater streams. We found an increase in macroinvertebrate abundance with higher amounts of phytobenthic biomass, suggesting a bottom-up effect through the food web in our study area. Similarly, higher levels of carbon and nutrients entering streams from permafrost thaw increasing benthic organic matter have been observed propagating through aquatic food webs in other Arctic streams of Alaska (Kendrick et al., 2018; Koch et al., 2018). Groundwater inflows to streams can have strong effects for benthic macroinvertebrate communities in headwater streams outside the Arctic (Wallace et al., 2015). For instance, a bottom-up effect was observed in the Pacific Northwest, USA, in which the exchange between groundwater and surface water drove differences in nutrients with subsequent effects on the productivity of algae and invertebrates, and ultimately bottom-up effects on juvenile fish growth (Mejia et al., 2016).

Macroinvertebrates, in combination with temperature, were identified as important to Dolly Varden biomass. One headwater stream (SFT1), however, was unique compared with the other headwater streams in the study design. One would not expect high Dolly Varden biomass in SFT1 due to the low density of macroinvertebrates, low amount of phytobenthic biomass, and low concentrations of carbon and nutrients, yet Dolly Varden biomass was high at SFT1. We explored if differences in temperature between the main stem river and tributary could explain the high amounts of Dolly Varden. Higher abundances of Dolly Varden in tributaries, as opposed to the main stem river, have been observed in Southeast, Alaska, USA (Bramblett et al., 2002), and other salmonids are known to optimize stream temperature along with foraging opportunities by moving between the main stem river and tributaries (Armstrong et al., 2010). However,

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we found no differences between temperatures in SFT1 and in the main stem river near the confluence of SFT1 (Carey et al., 2020). At certain flows, SFT1 is best characterized as a braided stream, which is unique among our headwater streams. It is possible that side channels and pools associated with the morphology of SFT1 could contain more productive resources that were not effectively captured by our sampling design. Our design focused on integrating the catchment of the headwater stream by collecting information on macroinvertebrate density, amounts of biofilm, and concentrations of carbon and nutrients near the confluence of the headwater stream and the mainstem river. Another possibility to explain the abundance of Dolly Varden is that the proximity of this unique headwater stream to spawning habitat in the main stem increases the amount of Dolly Varden in the area and using this stream. A resident population of Dolly Varden using this catchment is also a possibility, as both amphidromous and resident life history strategies occur in Alaska, USA (Carey et al., 2021). A detailed assessment of spawning habitat for Dolly Varden in these watersheds would allow a more complete understanding of their life history stages.

Overall, we found that permafrost characteristics drive stream hydrological and biogeochemical factors that influence fish in headwater streams. We suspect that the relations between near-surface permafrost and fish in headwater streams of northwest Alaska are applicable throughout the Arctic. These watersheds lie in the Arctic-boreal transition zone and estimates suggest near-surface permafrost will be reduced by half by 2100 in response to projected warming in the region (Panda et al., 2016). Understanding drivers of fish productivity improves our ability to predict the consequences of accelerating rates of permafrost thaw to stream food webs (Murdoch et al., 2021), especially given that headwater streams are large portions of river networks globally and provide important ecosystem services (Callahan et al., 2015; Colvin et al., 2019; King et al., 2012; Ward et al., 2020). Further developing our understanding of how these permafrost landscape changes influence Arctic ecosystems is imperative as Arctic air temperatures are increasing four times faster than the global average (Rantanen et al., 2022). Headwater streams in this region already show a warming trend and even minor warming may increase infiltration, subsurface flow, and drying, resulting in altered stream conditions (Koch, Sjöberg, et al., 2022; Sjöberg et al., 2021). Further changes from climate warming are likely to be substantial due to the simple trophic structure of Arctic food webs, suggesting the magnitude of effect from permafrost thaw on fish will likely increase in these headwater streams (Gough et al., 2016; Juhasz et al., 2020). Furthermore, the effects of permafrost thaw that create deeper flow paths, reducing surface waters and lowering summer water temperatures, are interacting with the warming effects from higher air temperature (Sjöberg et al., 2021). The complexities and interactions between warming effects may have nonintuitive outcomes requiring continued development of a process-based understanding of the hydro-ecological links to inform resource management decisions and forecast how ecosystems will respond to landscape dynamics.

AUTHOR CONTRIBUTIONS

Michael P. Carey, Joshua C. Koch, Jonathan A. O'Donnell, and Christian E. Zimmerman conceived the ideas and designed the study. Michael P. Carey, Joshua C. Koch, Jonathan A. O'Donnell, and Brett A. Poulin collected the field and laboratory data. Michael P. Carey analyzed and visualized the data with assistance from Joshua C. Koch and Jonathan A. O'Donnell. Michael P. Carey led the writing of the manuscript. All others contributed to data interpretation, provided critical input into manuscript drafts, and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sets utilized for this research (Carey et al., 2020, 2024, 2025; Carey, Koch, et al., 2023; Koch et al., 2019; O'Donnell et al., 2021) are available from the US Geological Survey ScienceBase-Catalog: https://doi.org/10.5066/P91HI62H; https://doi.org/10.5066/P9WGRX66; https://doi.org/10.5066/P90B3QO0; https://doi.org/10.5066/P1AIBLTB; https://doi.org/10.5066/P9EIX8ET; https://doi.org/10.5066/P9SBK2DZ.

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