

Glacier runoff influences biogeochemistry and resource availability in coastal temperate rainforest streams: Implications for juvenile salmon growth

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Abstract

Meltwater contributions to watersheds are shrinking as glaciers disappear, altering the flow, temperature, and biogeochemistry of freshwaters. A potential consequence of this landscape change is that streamflow patterns within glacierized watersheds will become more homogenous, potentially altering the capacity of watersheds to support Pacific salmon. To assess heterogeneity in stream habitat quality for juvenile salmon in a watershed in the Alaska Coast Mountains, we collected organic matter and invertebrate drift and measured streamwater physical and biogeochemical properties over the main runoff season in two adjacent tributaries, one fed mainly by rain and the other partially by glacier ice/snowmelt. We then used bioenergetic modeling to evaluate how temporal patterns in water temperature and invertebrate drift in each tributary influence juvenile salmon growth potential. Across the study period, average invertebrate drift concentrations were similar in non-glacierized Montana (0.33 mg m^{-3}) and glacier-influenced McGinnis Creeks (0.38 mg m^{-3}). However, seasonal patterns of invertebrate drift were temporally asynchronous between the two streams. Invertebrate drift and modeled fish growth were generally higher in McGinnis Creek in the spring and Montana Creek in the Summer. For juvenile salmon, tracking these resource asynchronies by moving between tributaries resulted in 20% greater growth than could be obtained within either stream alone. These results suggest that hydrologic heterogeneity within watersheds may enhance the diversity of foraging and growth opportunities for mobile aquatic organisms, which may be essential for supporting productive and resilient natural salmon runs.

The biomass and harvest of wild salmon in the North Pacific Ocean are currently near record highs, with nearly one-third of these salmon rearing in the coastal watersheds that ring the Gulf of Alaska (Irvine and Fukuwaka. 2011; Johnson et al. 2019). These salmon watersheds are undergoing complex climate-driven changes, including rising air temperatures, decreasing seasonal snowpacks, increasing streamflows during the winter months, and melting glaciers (reviewed by Bidlack et al. 2021). A potential consequence of this landscape change is that streamflow patterns in the region will become more homogenous with the loss of glacier- and snow-fed streams (Sergeant et al. 2020), thereby reducing freshwater habitat complexity and altering conditions for salmon to complete life cycles (Pitman et al. 2020; Bellmore et al. 2022). A thorough

understanding of how stream habitat conditions and food availability for salmon may respond to climate change is therefore critical to our understanding of the capacity of high-latitude coastal watersheds to support natural salmon runs.

Stream-dwelling salmon require a mosaic of habitat types within individual watersheds to support the various stages of their life cycle (Bellmore et al. 2013; Brennan et al. 2019). For instance, juvenile Pacific salmon feed extensively in cold aquatic habitats and then move to warmer stream habitats to help increase their assimilative capacity during digestion (Armstrong and Schindler 2013). Likewise, salmon may move upstream to small tributaries to capitalize on food availability (Wipfli and Gregovich 2002) and avoid energetically costly and potentially hazardous seasonal high flows in the watershed mainstem (Bramblett et al. 2002). Aquatic habitat complexity therefore creates differences in the temporal dynamics of prey availability and energetic demands across the river network that may provide enhanced growth opportunities for mobile consumers, such as fish (Wipfli and Baxter 2010; Armstrong et al. 2016, 2021; Bellmore et al. 2022).

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The temperate rainforest of coastal southeast Alaska contains a mosaic of rain-fed (typically organic matter-rich wetland streams) and meltwater-fed (snow and glacier melt) streams that can occur in close proximity to each other within individual watersheds, thereby providing a diversity of freshwater habitat conditions for fishes. In general, glacier-fed streams have high, cold, and turbid flows during the summer runoff months, whereas summer flows in rain-fed streams are typically lower (but more stochastic), warmer, and have higher light transmission (Milner et al. 2000; Hood and Berner 2009; Milner et al. 2017). Glaciers are particularly important contributors to streamflow in this region, as glacier runoff accounts for ~30% of total land-to-ocean regional discharge (Neal et al. 2010). However, many watersheds contain small glaciers that are not connected to larger accumulation zones (i.e., icefields) and thus are projected to disappear within the next few decades (Clarke et al. 2015; Ziemer et al. 2016). Indeed, many glacial watersheds around the Gulf of Alaska have already passed peak glacial meltwater runoff or will by the middle of the 21st century (Huss and Hock 2018).

Invertebrate drift is one component of stream food webs that maybe impacted by shifts in seasonal runoff patterns caused by the loss of glaciers (Saltveit et al. 2001; Schütz and Füreder 2018). Invertebrate drift has been widely studied in forested streams because it is frequently the main food source for salmonids (Allan et al. 2003). However, patterns of drift abundance in glacier streams are poorly studied and remain a fundamental gap in understanding the role glacier streams have in supporting salmon populations. It is possible that the distinct physical and biogeochemical properties found in glacial streams in coastal southeast Alaska (Hood and Berner 2009; Fellman et al. 2014a) may support distinct temporal patterns of drifting food availability and associated fish growth potential compared to rain-fed streams (Bellmore et al. 2022).

The goal of this study was to assess stream habitat quality as it relates to juvenile Pacific salmon growth potential in two adjacent tributary streams, one fed mainly by rain and the other partially by glacier ice and snowmelt. We collected organic matter (i.e., detritus) and invertebrate drift, and measured streamwater physical (temperature, flow, and turbidity) and biogeochemical properties (C, N, and P) during the main runoff season in both streams. Although detritus is not directly consumed by juvenile salmon, it supports the production of aquatic invertebrates that are a primary prey source for salmonids. We modeled juvenile salmon growth potential in each stream using temperature and our measurements of invertebrate drift to test the hypothesis that temporal patterns in temperature and food availability in forested and glacierized streams are distinct, and create asynchronous patterns in habitat quality for juvenile Pacific salmon. Our findings will be used to generate testable hypotheses on the impacts of climate warming on food availability and key environmental parameters that influence habitat quality for Pacific salmon in a

region where changes in glacier and snow cover are rapidly altering freshwater habitats.

Methods

Study area

The two study streams, Montana and glacier-influenced McGinnis Creek, are located near Juneau in the cool, maritime climate of southeast Alaska (Fig. 1). The study area sits in the northern portion of the coastal temperate rainforest, which extends along the coastal margin of the Pacific Northwest of the United States and British Columbia through the Gulf of Alaska. Multiple glacial periods have left southeast Alaska with a mixture of landscape features including glaciers, carbon-rich peatlands, and extensive temperate forest, which together store some of the highest amounts of carbon per unit area globally (Bidlack et al. 2021). The streams are located in the Montana Creek watershed, which has an area of 27 km² above the confluence of the two streams. The watershed sits on the western fringe of the 3800 km² Juneau Icefield (JIF), although the small hanging glaciers that feed McGinnis Creek are disconnected from the JIF. Glacier thinning rates on the JIF can exceed 5 m yr⁻¹ (Larsen et al. 2015) and the JIF is projected to lose roughly two thirds of its surface area by 2100 (Ziemer et al. 2016).

The drainage basin for the glacier-influenced McGinnis Creek tributary is 17.2 km², with 4% of its area covered by glacier ice and 40% by forest. The upper watershed accumulates an extensive seasonal snowpack and consists of recently deglaciated slopes with sparse vegetation and thin soils, while the lower watershed is an uplifted marine terrace with mature spruce (*Picea sitchensis*) and hemlock (*Tsuga heterophylla*) forest. The non-glacial Montana Creek drainage basin is 9.5 km² and has more subdued relief (average watershed slope of 18° compared to 25° for McGinnis Creek), which results in greater watershed wetland (7%) and forest coverage (85%) compared to McGinnis Creek. The geology in both watersheds is similar consisting of a mixture of volcanics, carbonates, granitic, and metamorphic rocks mainly from the Mesozoic. Multiple species of adult Pacific salmon (*Oncorhynchus* spp.) spawn in both tributaries from July through October, and juvenile Coho Salmon (*Oncorhynchus kisutch*) rear in both tributaries year-around.

Field sampling

Surface water from the McGinnis and Montana Creek tributaries was collected for concentrations of dissolved organic carbon (DOC), total dissolved nitrogen (TDN), inorganic N and P, turbidity, total suspended sediment (TSS), and stable isotopes of water ($\delta^{18}\text{O}$) at least twice per week from early May through the end of October of 2018. Streamwater samples were field-filtered through precombusted (450°C for 4 h) Whatman glass fiber filters (nominal pore size 0.7 μm) and placed in acid-washed polyethylene bottles for nutrient

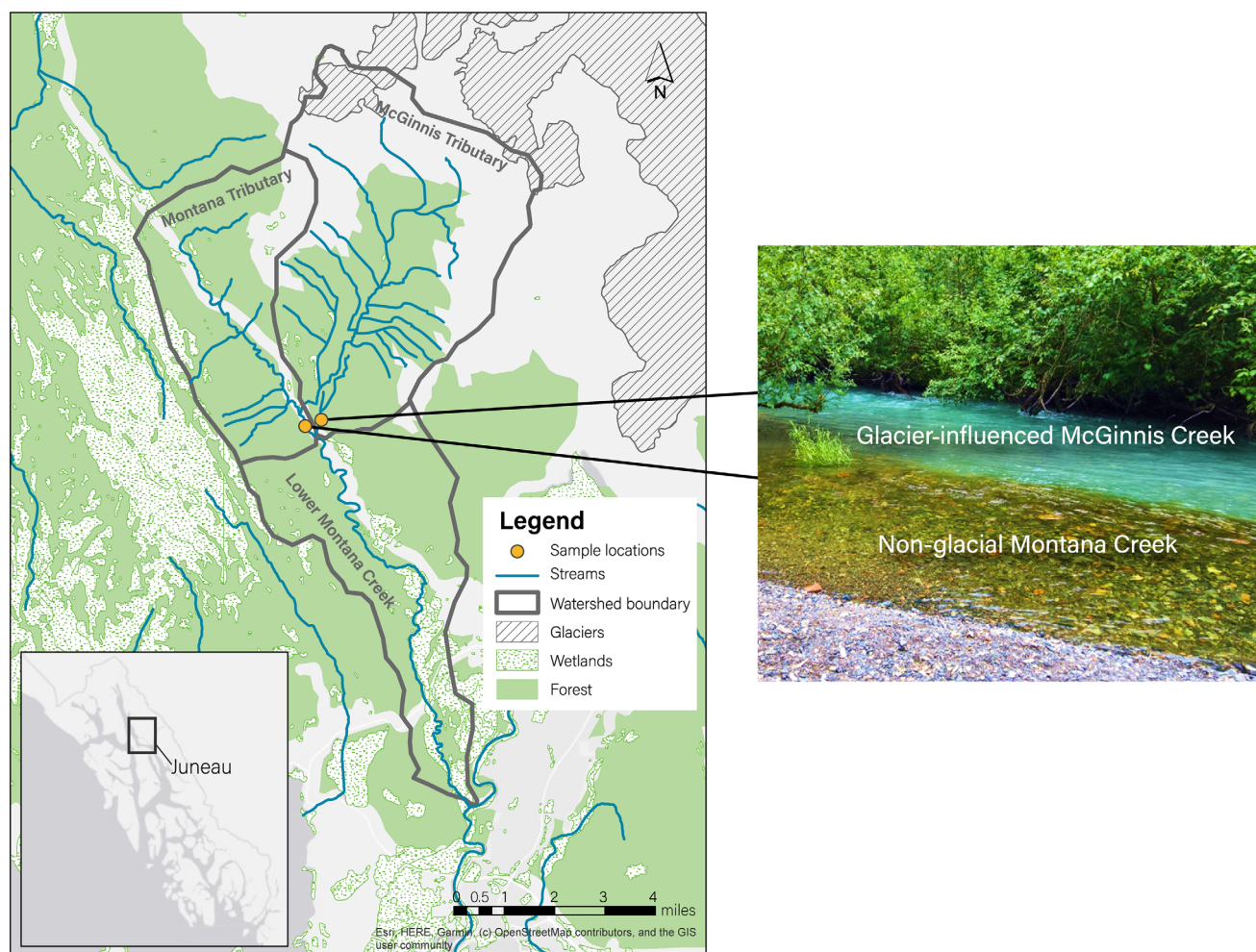


Fig. 1. Map of the study watersheds and sampling locations near Juneau, Alaska. Inset photo is of the confluence of the glacier-influenced McGinnis Creek and Montana Creek.

analyses and in precombusted (450°C for 4 h) glass vials for DOC analyses. Samples of DOC and TDN were analyzed within 48 h of collection while samples for nutrient analysis were frozen immediately and analyzed at a later date. Water isotope samples were collected unfiltered in glass bottles with zero headspace and stored at room temperature until analysis. Turbidity and TSS samples were collected in 2-L polycarbonate bottles and stored in the refrigerator until analysis within 48 h of collection. During each sample event, discrete measurements of stream temperature and specific conductivity were measured in the study reaches using a YSI hand-held (model 556) meter. Continuous stream temperature was also measured hourly at both sites using YSI EXO2 Sondes.

Streamwater drift samples were collected approximately weekly in both study streams by placing a 45 cm by 27 cm drift net (250 μ m mesh) level with the water surface to include both surface and water column drift. The drift net frames were supported by rebar that was hammered directly into the stream bed. Drift net sample collection ranged from 15 to 60 min, with shorter sets

occurring during periods of high flow to prevent clogging of the drift net. After drift sample collection, the removable cod-end was emptied into a 250- μ m sieve before being transferred into a whirl-pak, and preserved in 95% ethanol. Sample duration (sec), stream velocity (measured in m s^{-1} using a Geopack flowmeter), and wetted net depth (m) were recorded to calculate the volume of water sampled (m^3) using net dimensions [wetted area of opening (m^2) * water velocity (m s^{-1}) * sample duration (s)]. Water volume was used to quantify drift concentrations (mg m^{-3}).

Daily discharge was modeled in the McGinnis Creek tributary using linear regression between periodic flow measurements in the sample reach ($n = 15$, $r^2 = 0.91$) and discharge from a National Weather Service stream gage on Montana Creek located ~ 6 km downstream. Discharge in the Montana Creek tributary was measured directly using a SonTek Flowtracker current meter across a wide range of flows. Stream stage was recorded at 15-min intervals (using an In-Situ Level TROLL pressure transducer), and the resulting stage-discharge relationship was used to calculate streamflow.

Sample processing and analytical analyses

Concentrations of DOC (as non-purgable organic carbon) and TDN were analyzed by high-temperature combustion on a Shimadzu TOC/TN-V-CSH analyzer. Analytical precision (mean standard deviation for identical samples reanalyzed during analytical runs) was 0.02–0.04 mg C L⁻¹ for DOC and 0.1–0.2 mg N L⁻¹ for TDN. Nitrate (NO₃-N) and ammonium (NH₄-N) were measured colorimetrically at the University of New Hampshire Water Quality Analysis Laboratory. Dissolved organic nitrogen (DON) was calculated as the difference between TDN and dissolved inorganic N (DIN = NH₄-N + NO₃-N). Soluble reactive phosphorus (SRP) was measured using the ascorbic acid method (Murphy and Riley 1962) with a 5-cm quartz cell (lower detection limit 1–2 µg P L⁻¹).

Stable water isotope samples were analyzed on a Picarro L2120-I analyzer and δ¹⁸O values are reported in per mil (‰) after normalization to Vienna standard mean ocean water (VSMOW). Turbidity was measured in the laboratory using a HACH (2100P) turbidimeter. Concentrations of TSS (mg L⁻¹) were determined by passing a known volume of water through a precombusted (4 h at 450°C), preweighed, GF/F filter, and reweighed after drying for 24 h at 60°C. Filter blanks for TSS were also run using Milli-Q water following identical protocols.

Drift samples were processed by separating detritus from invertebrates in the lab using a dissecting microscope at 2× magnification. Large drift samples were split before sorting using a Motodo box-type sample splitter. The sorted detritus was dried for 24 h at 40°C, weighed and ashed at 450°C for 4 h. Once burning was completed, samples were rewetted with 2–5 mL of Milli-Q water and dried again for 24 h at 40°C, then reweighed to determine ash-free dry mass (AFDM). Separated invertebrates were identified to order, measured for body length and dry mass was determined using length/weight regression models (Benke et al. 1999; Sabo et al. 2002). Invertebrates were categorized as aquatic or terrestrial and life stage was documented if applicable.

Linear regression was used to assess relationships between drift concentrations, discharge, and streamwater δ¹⁸O values across the study period. If necessary, values were log transformed to satisfy the assumptions of linear regression. All statistical analyses were performed in SPSS software.

Modeled salmonid growth potential

The Wisconsin Bioenergetics model (Deslauriers et al. 2017) was used to model juvenile salmon growth rates using observed stream temperatures and invertebrate drift concentrations. The model was parameterized for juvenile Coho Salmon (*Oncorhynchus kisutch*), which are the most abundant juvenile salmon that reside year-round in southeast Alaska rivers. We constructed daily estimates of drift availability by assuming linear interpolation between weekly drift measurements. We assumed a Type II saturating relationship between invertebrate drift concentrations and fish consumption rates

(Haskell et al. 2017), with a half-saturation drift concentration value of 0.25 mg m⁻³ (i.e., value at which consumption is half the temperature corrected maximum; Bellmore et al. 2017). We first used the model to examine daily “growth potential” for juvenile Coho Salmon in each tributary, where growth potential is the balance of metabolic gains (food assimilation) minus metabolic costs (respiration and specific dynamic action; Warren and Davis 1967). In each tributary, daily growth potential values were used to model the size at time (predicted fish size at any given time during model runs) of an individual Coho Salmon for the duration of the study period. We assumed a starting fish size of 0.5 g, which is the approximate size of Age 0 Coho Salmon in late spring in Montana Creek (Kevin Fitzgerald, unpublished data). We then calculated the growth that juvenile Coho Salmon could accrue by moving between the two tributaries, perfectly tracking the location with the greatest growth potential through time. We interpret modeled growth as the theoretical potential to grow a single fish based on temperature and drifting food availability alone.

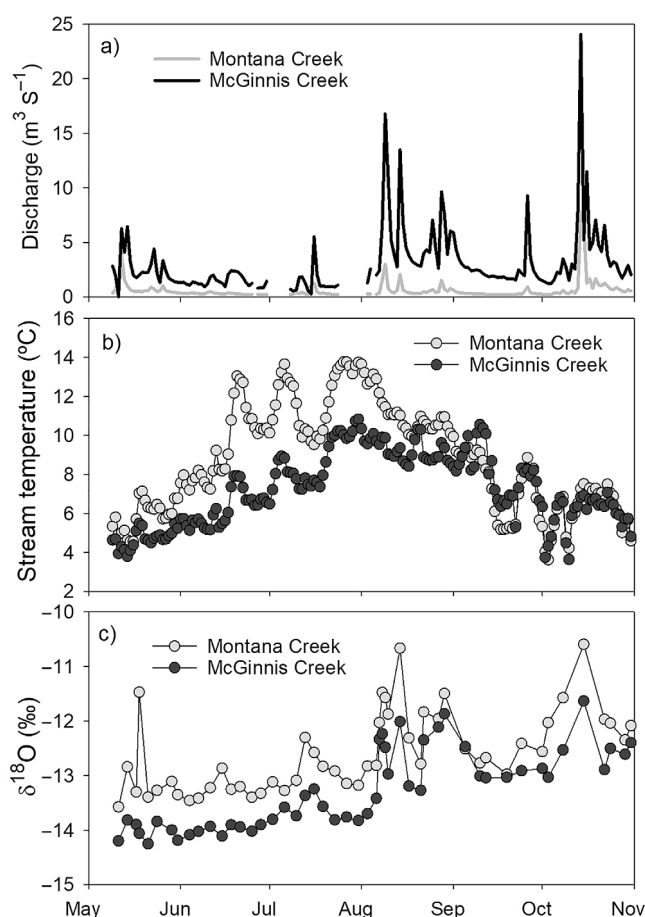


Fig. 2. Time series of mean daily (a) discharge, (b) stream temperature, and (c) streamwater δ¹⁸O values for glacier-influenced McGinnis Creek and Montana Creek across the study period. Missing discharge values occur during low flow periods when the pressure transducer went dry.

Results

Watershed hydrology and stream physicochemical properties

The seasonal hydrograph in lightly glacierized McGinnis Creek strongly reflected snow and ice-melt contributions to streamflow, especially during May and late summer (August/early September; Fig. 2a). However, in non-glacial Montana Creek, snowmelt inputs to discharge were only noticeable in May followed by several extended stretches of low flow in June and September when discharge was generally below $0.3 \text{ m}^3 \text{ s}^{-1}$. Mean daily stream temperature in Montana Creek ranged from 4.6°C to 13.8°C and showed higher variability compared to glacier-influenced McGinnis Creek, where temperature ranged from 3.8°C to 10.8°C (Fig. 2b).

Streamwater $\delta^{18}\text{O}$ values averaged -12.6‰ for Montana Creek and -13.3‰ for McGinnis Creek reflecting differences in the relative contributions of rainfall (enriched in $\delta^{18}\text{O}$) and snow/icemelt (depleted in $\delta^{18}\text{O}$) to runoff (Fig. 2c). In both streams, $\delta^{18}\text{O}$ values were the most depleted in May through July, but increased markedly thereafter and became more similar to previous reported values for rainfall in the area (-11.4‰ ; Fellman et al. 2014a,b). In addition, $\delta^{18}\text{O}$ values in both streams increased markedly during large storm events in August and October.

Specific conductivity in both streams showed no pronounced seasonal patterns, and values varied nearly fivefold across the study period (Fig. 3a). Streamwater turbidity and TSS concentrations were substantially lower (at least 2.5-fold) in Montana Creek relative to glacier-influenced McGinnis Creek across the study period (Fig. 3b,c). However, the CV for both parameters was slightly higher in Montana Creek

(turbidity = 1.7, TSS = 2.0) than in McGinnis Creek (turbidity = 1.6, TSS = 1.0) reflecting a proportionally greater response in sediment concentrations during rain events. Streamwater DOC concentrations ranged from a low of 0.28 mg C L^{-1} in McGinnis Creek to a high of 12.4 mg C L^{-1} in Montana Creek, with concentrations generally peaking during the rain events in July through October (Fig. 3d). In contrast, DON concentrations were slightly greater in McGinnis relative to non-glacial Montana Creek across the study period (Fig. 3e). Dissolved inorganic N was dominated by $\text{NO}_3\text{-N}$ in both streams (Fig. 3f), with substantially higher and more variable concentrations in the glacial stream (especially during May and October). Concentrations of $\text{NH}_4\text{-N}$ and SRP were low throughout most of the study period and comparable between both streams (Fig. 3g,h).

Streamwater drift detritus and invertebrate concentrations

Across the study period, average detritus concentrations were similar in Montana (28.4 mg m^{-3}) and glacier-influenced McGinnis Creek (28.7 mg m^{-3} ; Fig. 4a), despite more than two-fold greater relative forest cover in Montana Creek. Peak detritus concentrations in both streams occurred in August during a high-flow event, with concentrations increasing more than 10-fold in Montana Creek compared to the previous drift sample date. However, detritus concentrations were not correlated with mean daily discharge in either stream ($r^2 < 0.13$, $p > 0.37$).

The average concentration of drifting invertebrate biomass was similar for both Montana ($0.33 \text{ mg AFDM m}^{-3}$) and glacier-influenced McGinnis Creeks ($0.38 \text{ mg AFDM m}^{-3}$; Fig. 4b). The predominant taxa in the drift were also similar, with Plecoptera, Ephemeroptera, and invertebrates of

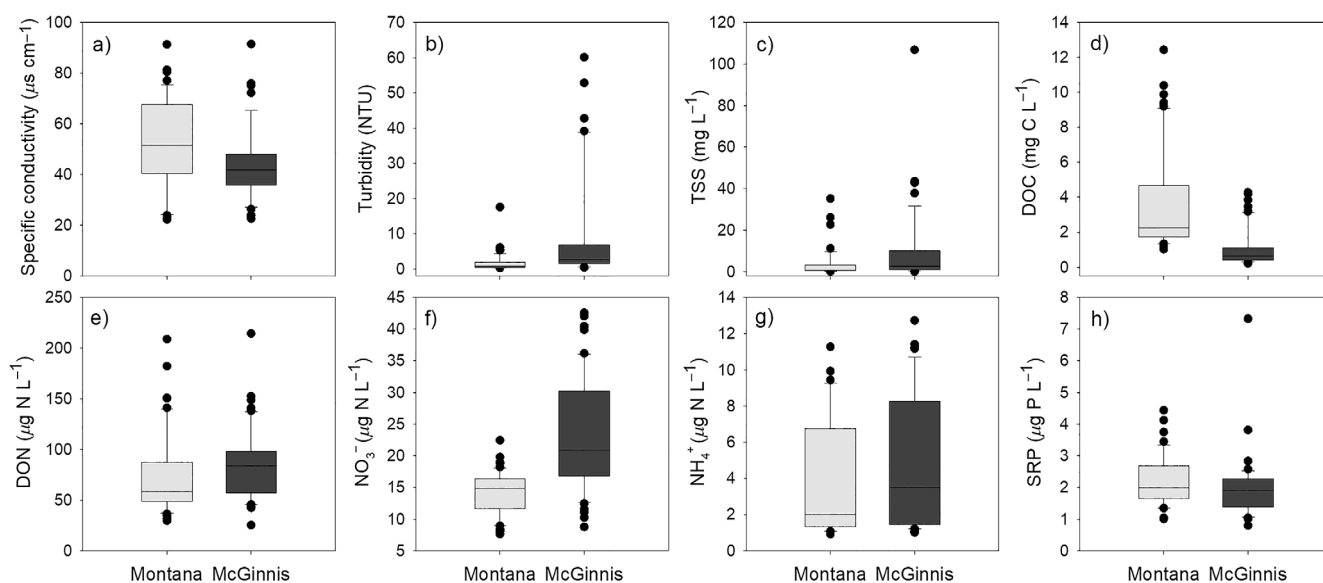


Fig. 3. Box plots of streamwater (a) specific conductivity, (b) turbidity, (c) TSS, and concentrations of (d) DOC, (e) DON, (f) NO_3^- , (g) NH_4^+ and (h) SRP in Montana Creek and glacier-influenced McGinnis Creek across the study period. The line within the box is the median, dots are the 10th and 90th percentile points and the vertical bars are the 25th and 75th percentiles.

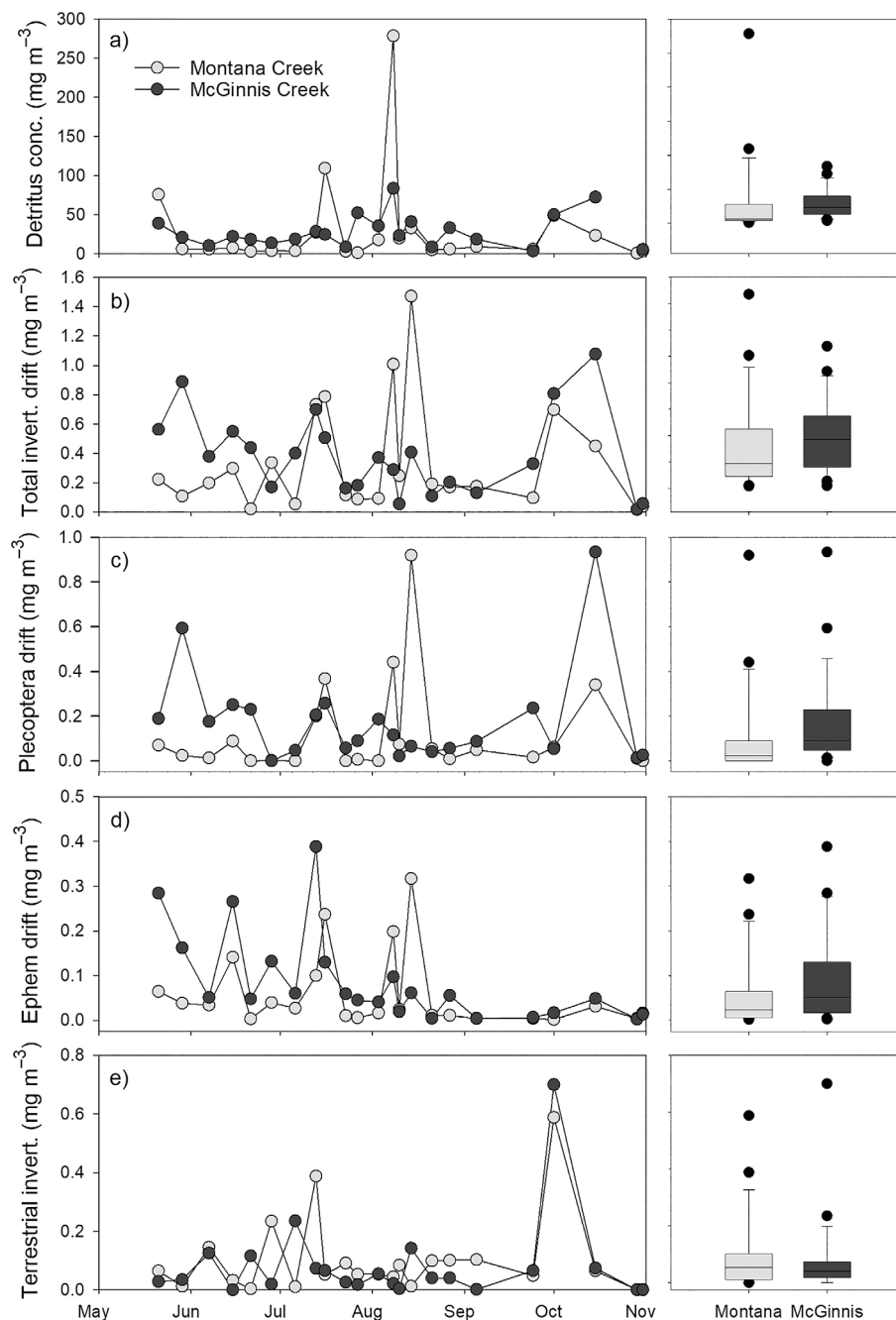


Fig. 4. Time series and box plots of drift (a) detritus concentrations, (b) total invertebrate concentrations, (c) Plecoptera concentrations, (d) Ephemeroptera (Ephem) concentrations, and (e) terrestrial invertebrate concentrations in Montana and glacier-influenced McGinnis Creek across the study period. The line within the box is the median, dots are the 10th and 90th percentile points and the vertical bars are the 25th and 75th percentiles.

terrestrial origin (largely Hymenoptera) representing at least 84% of the total invertebrate drift from both streams (Fig. 5). However, the temporal pattern of drift availability differed slightly between streams (Fig. 4b). Glacier-influenced McGinnis Creek had similar or generally greater invertebrate drift concentrations in the Spring (May and early June) and again in early Autumn (Sept and Oct), whereas concentrations

were similar or generally higher in Montana Creek in the summer months of July and August. Across all sampling dates, these temporal asynchronies resulted in McGinnis Creek having higher invertebrate drift concentrations roughly two-thirds of the time. Seasonal patterns of Plecoptera and Ephemeroptera abundance were largely responsible for this seasonal asynchrony in drift concentration (Fig. 4c,d). Average

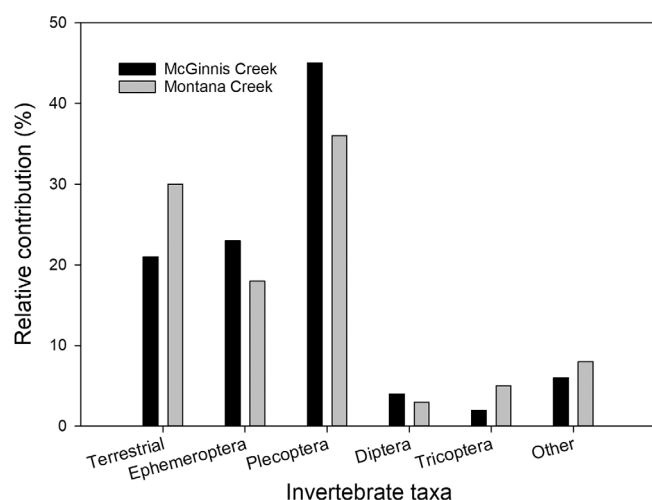


Fig. 5. The percent contribution of the predominant invertebrate taxa in non-glacial Montana and glacier-influenced McGinnis Creek across the study period.

terrestrial invertebrate drift concentrations were slightly greater but less variable (0.10 mg m^{-3} , $\text{CV} = 1.4$) in glacier-influenced McGinnis Creek than in Montana Creek (0.08 mg m^{-3} , $\text{CV} = 1.8$, Fig. 4e).

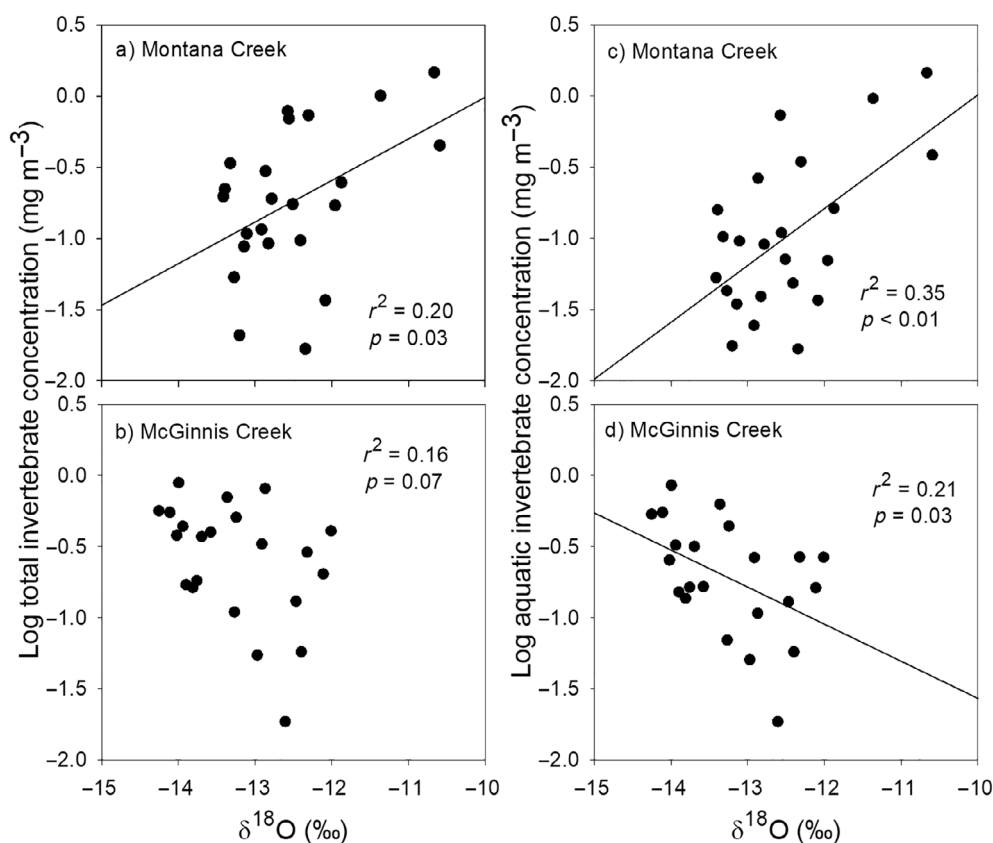


Fig. 6. Streamwater $\delta^{18}\text{O}$ values vs. drift total invertebrate concentration in (a) Montana Creek and (b) glacier-influenced McGinnis Creek and $\delta^{18}\text{O}$ values vs. drift aquatic invertebrate concentration in (c) Montana and (d) McGinnis Creek. Invertebrate concentrations were log transformed to satisfy the assumptions of linear regression.

We found no relationship between invertebrate drift concentrations and discharge in either stream, except during the month of August in Montana Creek where there was a strong positive correlation between discharge and invertebrate concentrations ($r^2 = 0.97$, $p < 0.01$, $n = 6$; data not shown). Streamwater $\delta^{18}\text{O}$ values were correlated with invertebrate drift concentration in Montana Creek ($r^2 = 0.20$, $p = 0.03$; Fig. 6a), but not in glacier-influenced McGinnis Creek ($r^2 = 0.16$, $p = 0.07$; Fig. 6b). Streamwater $\delta^{18}\text{O}$ values were also related to aquatic invertebrate drift concentrations in both Montana ($r^2 = 0.35$, $p < 0.01$) and McGinnis Creek ($r^2 = 0.21$, $p = 0.03$; Fig. 6c,d). However, the direction of the relationship was different, suggesting the main sources of streamwater impacted aquatic invertebrate abundance differently in the two streams.

Salmon growth potential

Modeled rates of daily juvenile Coho Salmon growth potential from measured invertebrate drift and stream temperature varied between the two stream types, but total seasonal growth was similar between the streams (Fig. 7). Although average daily growth over the course of the study period was identical (0.22 g d^{-1}) in both streams, growth potential was

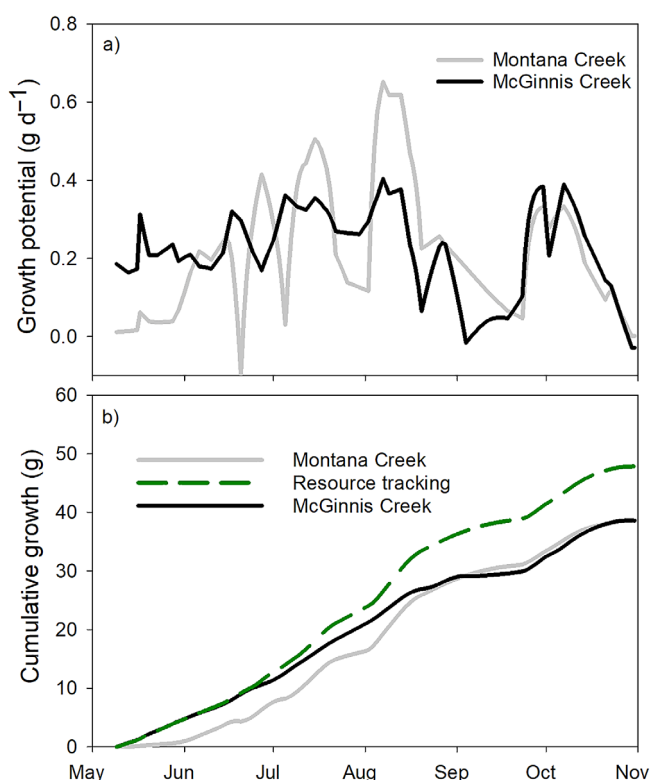


Fig. 7. Modeled (a) daily salmon growth potential and (b) cumulative salmon growth potential using drift invertebrate biomass and stream temperature in Montana and glacier-influenced McGinnis Creek across the study period.

more variable in Montana ($CV = 0.74$) relative to glacier-influenced McGinnis Creek ($CV = 0.49$). Fish growth potential in Montana Creek was frequently well above or below growth potential in the more stable glacier fed McGinnis Creek, especially during the summer (June–August; Fig. 7a). In the resource tracking model, fish grew 20% larger when they were allowed to move between the two streams tracking locations with the greatest growth potential (Fig. 7b). Most of the early season growth was driven by higher daily growth in McGinnis Creek followed by higher growth rates in Montana Creek during the summer, particularly in August, which allowed for enhanced cumulative growth in our analysis.

Discussion

Impacts of seasonal glacier discharge on stream chemical and physical properties

In southeast Alaska, the abundance of carbon-rich wetlands together with glacial and snowmelt fed tributaries creates substantial hydrologic heterogeneity within coastal watersheds. Streamwater DOC concentrations in Montana Creek were consistently higher than in lightly glacierized McGinnis Creek, as observed in other non-glacial watersheds in the Pacific coastal

temperate rainforest (Oliver et al. 2017; Edwards et al. 2021). On the other hand, SRP concentrations were similar between streams, but higher DIN concentrations were observed in McGinnis Creek. These results suggest that the retreat of the McGinnis Creek glacier reduced the delivery of P to surface waters that is typically caused by glacial weathering of mostly calcite/apatite-rich minerals (Hodson et al. 2004) and at the same time exposed new areas of the watershed that could be colonized by N-fixing plant species (Chapin et al. 1994), which can contribute abundant NO_3^- to streamwater (Compton et al. 2020). Within this context, our findings showed less striking differences in C, N, and P concentrations than previously reported in glacierized watersheds in the Pacific coastal temperate rainforest (Hood and Berner 2009; Fellman et al. 2014a; Behnke et al. 2021), likely as a result of the low watershed ice coverage ($\sim 4\%$) in McGinnis Creek.

The seasonal patterns in $\delta^{18}\text{O}$ values in the glacial stream are consistent with an increase in the proportion of streamflow-derived from $\delta^{18}\text{O}$ -depleted snow and ice melt in the higher elevation reaches of the watershed during the summer melt season (Mark and McKenzie 2007; Fellman et al. 2014a). This glacier discharge decreased water temperature an average of 1.6°C across the study period relative to the non-glacial stream suggesting that runoff from glaciers and snowfields moderates stream temperature even at low glacier coverage (Fellman et al. 2014b; Winfree et al. 2018). Future reductions in glacier volume in some glacier-dominated streams may actually enhance salmon growth potential by improving thermal suitability (Fellman et al. 2014b; Pitman et al. 2020). Glacial discharge to McGinnis Creek also increased turbidity and TSS by more than 2.5-fold compared to the non-glacial stream, with potentially wide-ranging impacts on salmon habitat quality (Pitman et al. 2020). For instance, elevated turbidity could reduce light penetration into the water and decrease primary productivity (Uehlinger et al. 1998; Füreder et al. 2003), limit visual foraging success by juvenile salmon (Lloyd et al. 1987), but also provide cover for juvenile salmon from visual predators (Young and Woody 2007).

Seasonal drift concentrations and transport

The study streams were conduits for detritus transport, with concentrations (< 0.01 – 0.28 g m^{-3}) similar to other forested streams in southeast Alaska (0.05 – 0.24 g m^{-3} , Wipfli and Gregovich 2002; 0.01 – 0.07 g m^{-3} , Wipfli and Musslewhite 2004), although substantially less than reported from temperate deciduous forested watersheds (0.5 – 4.0 g m^{-3} , Wallace et al. 1982). Concentrations of invertebrate drift ranged from < 0.1 – 1.5 mg m^{-3} , which is in the range of previously reported values for forested watersheds of southeast Alaska (< 1.0 – 60.0 mg m^{-3} , Wipfli and Gregovich 2002; 0.1 – 1.0 mg m^{-3} , Wipfli and Musslewhite 2004), Oregon (0.15 – 0.7 mg m^{-3} , Weber et al. 2014), and southeastern Georgia (< 0.1 – 1.8 mg m^{-3} , Benke et al. 1986). These results show that drift transport from forested and lightly glacierized watersheds in the Pacific coastal temperate

rainforest can contribute substantial amounts of organic matter to downstream reaches, and likely serve as “resource sheds” that support downstream and nearshore marine production (Power and Rainey 2000; Wipfli and Baxter 2010; Whitney et al. 2018).

Our finding that both streams had similar concentrations of drifting invertebrates supports other studies showing that although glacial headwaters are cold and turbid for much of the year, they can be productive ecosystems in terms of invertebrate biomass (for some invertebrate taxa) and transport to downstream ecosystems (Milner et al. 2000; Saltveit et al. 2001; Schütz and Füreder 2018). McGinnis Creek had elevated invertebrate drift concentrations (relative to non-glacial Montana Creek) in May and early June. Elevated primary and invertebrate production has been observed in other glacial-fed streams (Burgherr and Ward 2001; Saltveit et al. 2001; Schütz and Füreder 2018) during the non-melt season as a result of the more favorable environmental conditions (e.g., more stable stream bed, minimal sediment transport and low turbidity, elevated N and P concentrations) that generally persist during these periods (Uehlinger et al. 1998; Hood and Berner 2009; Ren et al. 2019; Sertić Perić et al. 2021).

The pattern of asynchronous resource dynamics in glacier-influenced McGinnis Creek (invertebrate drift was similar or higher in spring and again in early Autumn) and Montana Creek (drift was similar or higher in July and August) was driven in part by seasonal variability in Plecoptera and Ephemeroptera abundance in both streams. Thus, intra-watershed resource availability, which integrates resource dynamics across multiple tributaries, is likely to be less temporally variable than resource availability found within individual stream types. If glacial and rain-fed streams co-occur within close proximity in an individual watershed, peaks and troughs of resource availability in any single reach could be offset by asynchronies conditions elsewhere within the watershed (Bellmore et al. 2022).

Terrestrial invertebrates accounted for 21% and 30% of invertebrate drift in McGinnis and non-glacial Montana Creek, respectively, which was similar to other estimates in forested headwater streams of southeast Alaska (25%, Wipfli and Musslewhite 2004). It is generally thought that autochthonous production dominates carbon inputs to most mountain glacier streams because headwater reaches typically do not contain extensive riparian forests (Zah and Uehlinger 2001; Sertić Perić et al. 2021). However, in the low-elevation reaches of glacier watersheds common to the Pacific coastal temperate rainforest, dense riparian forests dominated by deciduous trees rapidly colonize recently deglaciated landscapes (Chapin et al. 1994; Milner et al. 2007) and may be a major source of terrestrial invertebrates to streams (Flory and Milner 1999; Milner et al. 2000).

Hymenoptera was the most common terrestrial invertebrate taxa in both study streams, as observed in other temperate forested streams in the United States (reviewed by Baxter et al. 2005). Terrestrial invertebrate subsidies to stream food

webs can be substantial (Wipfli 1997) and are often the preferred prey of juvenile salmonids (Baxter et al. 2005), especially during periods of low aquatic invertebrate production. Drifting terrestrial invertebrates were highly variable in the study streams, but the highest concentrations occurred in early October. These allochthonous organic matter subsidies in autumn may provide a timely energy source for juvenile salmon prior to overwintering because young-of-the-year salmonids can expend > 40% of their lipid reserves during the winter months (Berg and Bremset 1998). Collectively, our findings suggest that the combination of aquatic and terrestrial invertebrate drift likely work in unison to sustain salmon productivity within a watershed.

We could not attribute invertebrate and detritus export from both streams to any specific factor such as benthic invertebrate production and densities (Kennedy et al. 2014), rates of primary production (Benson et al. 2013), or physical factors such as local habitat (e.g., pool vs. riffle) and river geomorphology because we did not measure any of these parameters. In particular, invertebrate abundance was not related to discharge in either stream across the study period, although previous research has shown strong correlations between drift biomass and discharge in forested watersheds (Kennedy et al. 2014; Hayes et al. 2019). We did not specifically attempt to measure drift export at high resolution during high-flow events, thus it is possible that our sampling design failed to capture short-term (e.g., daily and sub-daily) variations in discharge–drift relationships.

The relationships between drift biomass and $\delta^{18}\text{O}$ values suggest that sources of streamwater ($\delta^{18}\text{O}$ -depleted snow and ice melt vs. more enriched rain water) may be influential in drift export. It is important to recognize that sources of streamwater are not driving the patterns in drift abundance but are indicators of watershed-scale processes, such as in-stream production, that may influence the relationship between $\delta^{18}\text{O}$ and drift abundance. In non-glacial Montana Creek, aquatic invertebrate biomass was positively related to streamwater $\delta^{18}\text{O}$ values suggesting that during large storm events where streamwater was enriched by rainfall, aquatic invertebrates were dislodged from streambed gravels and exported downstream (Gibbins et al. 2007). In contrast, regression analysis showed that aquatic invertebrate drift concentrations in glacial-affected McGinnis Creek were frequently highest when streamwater $\delta^{18}\text{O}$ values were depleted, suggesting that elevated aquatic invertebrate drift occurs during the spring snowmelt period (May through June). One potential explanation for this pattern is elevated rates of primary and invertebrate production that can occur during the non-peak icemelt season in glacier streams as a result of generally lower discharge (except during large storm events) and more favorable environmental conditions, such as low turbidity and minimal sediment transport (Burgherr and Ward 2001; Saltveit et al. 2001; Schütz and Füreder 2018).

Salmon growth potential and resource tracking

Our findings show that the co-occurrence of a rain and snow/ice fed streams in a watershed could enhance the growth of mobile consumers, such as juvenile Pacific salmon. In our bioenergetics model simulations, cumulative fish growth was 20% greater when fish tracked asynchronous peaks in growth potential between streams. Similar to patterns of drifting invertebrates, growth potential was generally higher in the glacier-fed McGinnis creek in the spring (May and parts of June), but switched to higher growth potential in Montana Creek in August and September. Our analysis also suggests that there may be ephemeral windows of high growth potential, lasting only a few days, in each stream that may provide important growth opportunities for mobile fishes (Fig. 7).

Although we did not empirically examine fish growth or movements, studies show that stream salmonids can indeed make directed movements to capitalize on foraging and growth opportunities (Ruff et al. 2011). Juvenile Coho Salmon can move over a kilometer in a single day to capitalize on ephemeral peaks in food availability (Armstrong et al. 2016), and directed movements to track marine resource subsidies enhance growth in rainbow trout (Ruff et al. 2011). In southeast Alaska, juvenile salmon can move from mainstem habitats to small tributaries during floods (Bramblett et al. 2002), potentially capitalizing on terrestrial invertebrate fluxes from these small fishless tributaries (Wipfli and Gregovich 2002). Therefore, fishes that reside near or just downstream of tributary junctions, like the McGinnis-Montana confluence, could integrate these asynchronies in food availability with very little movement. Overall, when assessing freshwater habitat quality for juvenile salmon, it may be necessary to consider more than single habitats or time periods, but the mosaic of growth potential phenologies provided by diverse freshwater habitats across the river network (Bellmore et al. 2022; Cordoleani et al. 2022).

Temperature and food-driven bioenergetics models, such as the one we use in this study, offer an appealing tool for evaluating stream salmon habitat quality because they are linked to the major physiologic processes that control salmonid growth (Weber et al. 2014). However, our analysis ignores aspects of fish foraging and metabolism that are frequently included in more complex bioenergetic approaches, such as water turbidity, water velocity and depth, fish density, and diurnal and spatial variation in prey availability (Railsback et al. 2009; Wall et al. 2016). Including these factors would potentially reduce fish growth below what we predict based on temperature and invertebrate drift alone. For instance, many salmon and trout foraging models assume that higher water turbidity, such as found in glacier-fed McGinnis Creek, reduces foraging and growth (Hayes et al. 2007; Naman et al. 2020). That said, fish gut content analysis suggests that salmon and trout can successfully forage despite high turbidity in glacier-fed streams (>100 NTU; Matthew Dunkle, unpublished data), an

observation that is corroborated by published studies that have examined turbidity impacts on salmonids (White and Harvey 2007; Harvey and Railsback 2009). Despite the limitations of our analysis, our findings provide the foundation for future empirical efforts to examine the capacity for juvenile salmon to track foraging and growth opportunities between meltwater and non-meltwater streams in the Gulf of Alaska.

Impacts of cryospheric change on stream food webs in coastal Alaska

Glaciers in the Coastal Mountains of southeast Alaska are currently losing ice mass at elevated rates relative to other mountain regions and are projected to continue losing mass at high rates in the future (Radić and Hock 2011; Ziemen et al. 2016). Regional climate is also expected to warm, with an increasing proportion of precipitation falling as rain rather than as snow (Shanley et al. 2015). Thus, climate change is expected to simplify watershed hydrology through the reduction and/or loss of seasonal glacial and snowmelt inputs to watershed flow networks. Our findings indicate that physico-chemical conditions and associated resource availability across the landscape might become more synchronous with the loss of these cryospheric-fed tributaries, thereby decreasing habitat and resource heterogeneity and potentially the capacity of watersheds to provide favorable year-round habitat for juvenile salmon. Although glacial retreat and associated changes to flow regimes and stream environmental conditions are reducing suitable freshwater habitat for Pacific salmon, glacier loss is mitigating some of these impacts by creating new streams and lakes for salmon to colonize across their range (Pitman et al. 2020). Overall, our findings indicate that diverse and connected salmon habitat within watersheds are essential for supporting productive and resilient natural salmon runs (Brennan et al. 2019). Adaptation and mitigation strategies customized around rapidly changing northern ecosystems and the loss of terrestrial land ice will therefore fill a critical role in maintaining freshwater productivity and sustainable salmon fisheries.

Data availability statement

All data in this study are available online (<https://kn.b.ecoinformatics.org/view/doi:10.5063/F1B56H6F>) through DataONE Environmental Data Initiative.

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Conflict of Interest

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